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Seasonal Variation in Use of Time
and Space by the Wedge-capped
Capuchin Monkey, *Cebus olivaceus*:
Implications for Foraging Theory

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JOHN G. ROBINSON

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Seasonal Variation in Use of Time
and Space by the Wedge-capped
Capuchin Monkey, *Cebus olivaceus*:
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John G. Robinson



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ABSTRACT

John G. Robinson. Seasonal Variation in Use of Time and Space by the Wedge-capped Capuchin Monkey, *Cebus olivaceus*: Implications for Foraging Theory. *Smithsonian Contributions to Zoology*, number 431, 60 pages, 23 figures, 16 tables, 1986.—The relationship between the foraging behavior of a group of wedge-capped capuchin monkeys *Cebus olivaceus* and the abundance and spatial distribution of resources, was examined in a highly seasonal gallery forest in central Venezuela during 14 months. The aim of the study was to evaluate the behavioral mechanisms regulating group foraging. How the group forages depends on the information that animals possess about resource availabilities in their home range. Can the foraging behavior be predicted by assuming that animals know about resource abundances (both in areas where the animals are and for the whole area), the spatial distribution of specific resources, or the actual locations and qualities of specific resources?

The composition of the diet varied seasonally, with animals being less selective in periods of scarcity. The amount of time that animals forage increases with resource abundance, but only in the dry season, when food is scarce. During the wet season, foraging time is determined by the digestive capacities of the animals. The pattern of group movements and use of space do not depend on the amount of time that animals forage, the proportion of time allocated to foraging on specific items, or the spatial distribution of resources, but they are predictable from the specific distribution, both the patchiness and clumping of patches, of the most common resource available each month.

Foraging groups of capuchin monkeys thus have considerable information on resource location and quality and navigate over their ranges on the basis of that knowledge. This capacity is advantageous in a species that exploits ripe fruit, a resource that varies predictably in time and space. Large ranges ensure that fruiting species are available throughout the year. Because group ranges overlap completely and groups compete for access to fruiting trees, groups are large.

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Contents

	<i>Page</i>
Introduction	1
The Study Site	2
Acknowledgments	2
Methods	3
Abundance and Distribution of Resources	3
Identification	3
Relative Density	3
Spatial Distribution	4
Phenology	6
Behavioral Sampling	7
Diet	7
Time Budgets	8
Movements and Use of Space	8
Results	11
Abundance and Distribution of Resources	11
Relative Density	11
Spatial Distribution	11
Seasonal Variation	11
Diet	18
Vegetative Material	18
Flowers and Fruits	18
Invertebrates	21
Vertebrates	23
Seasonal Variation	23
Time Budgets	26
Seasonal Variation	28
Movements	33
Seasonal Variation	36
Use of Space	40
Seasonal Variation	42
Discussion	47
Diet	48
Use of Time	48
Group Movements and Use of Space	48
Group Size	49
Appendices	51
Appendix I: Glossary of <i>Cebus olivaceus</i> Foraging Actions	51
Appendix II: Microhabitats	52
Appendix III: Plant Species Used by Capuchins	54
Literature Cited	56

Seasonal Variation in Use of Time and Space by the Wedge-capped Capuchin Monkey, *Cebus olivaceus*: Implications for Foraging Theory

John G. Robinson

Introduction

In primates, social characteristics of species, such as their typical group size and composition, can be generally predicted by considering only their diet and the habitat in which they live (Crook and Gartlan, 1966; Eisenberg et al., 1972). Group size and composition are, in part, responses to how animals forage (e.g., Eisenberg et al., 1972; Clutton-Brock, 1974; S. Altmann, 1974); how animals forage are responses to the spatial distribution of resource abundance (e.g., S. Altmann, 1974; Bradbury and Vehrencamp, 1976; Waser and Wiley, 1979); and resource distributions are a direct consequence of the habitat and diet of a species.

This study of the wedge-capped capuchin monkey *Cebus olivaceus* (= *nigrivittatus*, following Honacki, Kinman, and Koepl, 1982) examines how social groups of this species forage for food. It focusses on the amount and kind of information that animals possess on the temporal and spatial distribution of resource abundance in their range. I consider four kinds of information.

1. Do animals know *what* resources are available at any moment in time? Such knowledge is required, for example, by several models of optimal diet choice (MacArthur and Pianka, 1966; Emlen, 1966; Schoener, 1971; Charnov, 1976).

2. Do animals know the *abundance* of available resources, in both the area in which they are foraging and over their range as a whole? Such information is required by models of optimal time allocation (Pyke et al., 1977; Krebs, 1979).

3. Do animals know the *spatial distribution* of available resources? This information might be restricted to only knowing whether a specific resource is patchily distributed in space, and whether the patches themselves are clumped in space. Such information is required by some search models (Smith, 1974a, 1974b; Thomas, 1974; Zach and Falls, 1977; Krebs, 1979).

4. Do animals know the *location* of available resources? If they have this information, animals must have a long-term spatial memory. Such information is required by certain optimal movement models (S. Altmann, 1974; Montgomery and Lubin, 1977; Kamil, 1978).

How groups of capuchin monkeys forage should depend on their access to the appropriate information, and their ability to take advantage of that information. For instance, if animals know

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where resources are located they need not search for them, and this should affect what animals eat and how they should move. In this study of capuchin monkeys, monthly variation in their diet, time budgets, movements, and use of space was used to test predictions developed from different expectations of what the monkeys know about their resources.

THE STUDY SITE.—The study site, Fundo Pecuario Masaguaral, is an active cattle ranch located as 8°34'N, 67°35'W in the *llano intermedio* savanna plains of central Venezuela. This ranch, owned by Sr. Tomas Blohm, has been maintained as a wildlife refuge since 1944. The vegetation on the ranch has been described by Troth (1979, in prep.) and Wiley and Wiley (1980), and consists of a mosaic of grasslands, palm savannas, shrub woodland, and gallery forest.

Capuchin monkeys inhabit the gallery forest bordering two rivers, the Caño Caracol and the Rio Guarico, in the extreme eastern part of the ranch. In this area the continuous gallery forest averages 4–5 km in width. Trees only occasionally reach heights over 20 m. As the canopy is not completely closed, the understory is well developed, and conspicuous layering is absent. Bordering the Rio Guarico, trees are taller; the maximum height recorded is 38 m (Mader, 1979). As one moves away from the rivers the forest grades into shrub woodland and grassland. The flora of nearby riparian forests have been described by Aristeguieta (1966), Ramia (1974), and Castillo (1977).

Most of the *llanos* of Venezuela, including this site, have been classified, using the Holridge system (Ewel et al., 1976), as dry tropical forest. It is, however, more grassland than forest. The *llanos* are characterized by a pronounced seasonality that strongly affects resource availability. Total yearly precipitation at this site averages about 1,450 mm, but most of that total falls during six months of the year (May through October). During the dry season, temperatures are more extreme and the mean temperature is higher (Figure 1). Relative humidity averages about 40% (Robinson, 1979). Most plant species

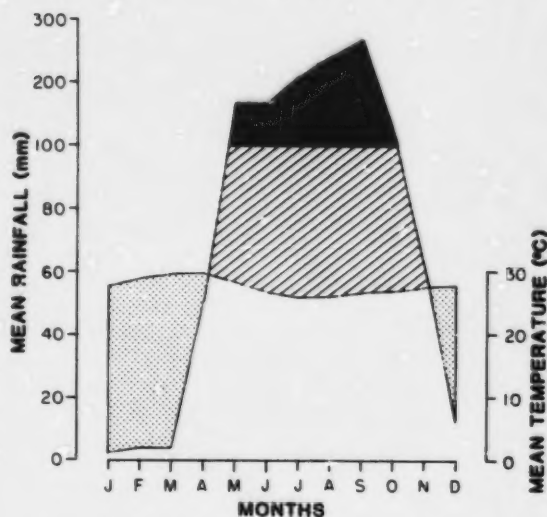


FIGURE 1.—Climate diagram (see Walter, 1971) of the Venezuelan central *llanos*, indicating period of drought (stippled) and period of rainfall superabundance (black). Data for Los Llanos meteorological station, Calabozo, monthly averages 1968–1977.

are at least partially deciduous during this time (see Monasterio and Sarmiento, 1976). In the wet season, mean temperature and mean maximum temperatures are lower because of the frequent cloud cover. Relative humidity averages close to 80%.

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suggested the study and was a constant source of information and encouragement. Tomas Blohm provided accommodation and never-ending logistic support at his ranch, Hato Masaguaral. Devra Kleiman unswervingly supported the research, the analysis, and its publication. Colleagues and friends at the ranch were unselfish with their time and energy: Gay Troth Ovrebo helped with collections and provided most of the botanical identifications; Yael Lubin did the same for invertebrates; Rudy Rudran provided indefatigable assistance with field problems and sampling design; and Pete August kept the roads open and reported every capuchin anomaly. Antonio Angel Aquino cut, marked, and tagged trails, identified trees, and ran vegetation transects. My wife Linda Cox sustained me through all the stages. Discussions and comments on versions of the manuscript involved many people, but especially P. August, C. Crockett, J. Eisenberg, D. Frigaszy, D. Moskovits, K. Redford, and P. Waser.

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Methods

ABUNDANCE AND DISTRIBUTION OF RESOURCES

While capuchin monkeys eat both plant and animal material (mostly invertebrates), little effort was made to sample the temporal and spatial distribution of invertebrates. This was because plant material makes up the bulk of the diet of capuchin monkeys (see Hladik and Hladik, 1969), and it is the spatial distribution of fruit

trees rather than invertebrates that should affect how the animals forage. I reasoned that from a capuchin monkey's perspective, invertebrates are relatively homogeneously distributed in space. They are not totally uniformly distributed, for certain microhabitats, such as palm crowns, rotting wood, and leaf litter are particularly rich in invertebrates taken by capuchins. But rich invertebrate microhabitats are only separated by tens of meters, while fruit trees are likely to be hundreds of meters apart. Thus, if monkeys respond to resource distributions, their use of time and space should be more affected by the spatial distribution of fruit trees than by that of invertebrates.

IDENTIFICATION.—All woody plant species in the gallery forest were identified by a knowledgeable herbalist and ranch worker in the field, using local names. Most identifications relied on bark and leaf characteristics. When each species flowered and fruited, voucher specimens were collected, dried, and subsequently identified at the herbarium of the Instituto Botanico in Caracas. This allowed me to equate scientific names with local names. Definitions of taxa were almost identical using the two systems. Invertebrates were collected opportunistically in the field and identified by entomologists working at the field station. This list was then used to identify what the monkeys were eating in the field.

RELATIVE DENSITY.—Relative density of a species is the number of individuals of that species divided by the total number of individuals of all species in the sample (Curtis and McIntosh, 1951). These values were calculated from tree enumerations along 14,400 m of transects. All transects followed existing north-south trails (Figure 2), and were spaced 100 m apart to cover most of the home range of the study group. I tallied all trees that occurred within 2.5 m of the trail (a strip 5 m wide) and had a crown height of 4 m or higher. I also recorded the heights of all individuals of two species of woody shrubs/understory trees, *Psychotria anceps* and *Randia hebecarpa*, that had a height of 2 m or higher. The fruits of these two shrubs were an important

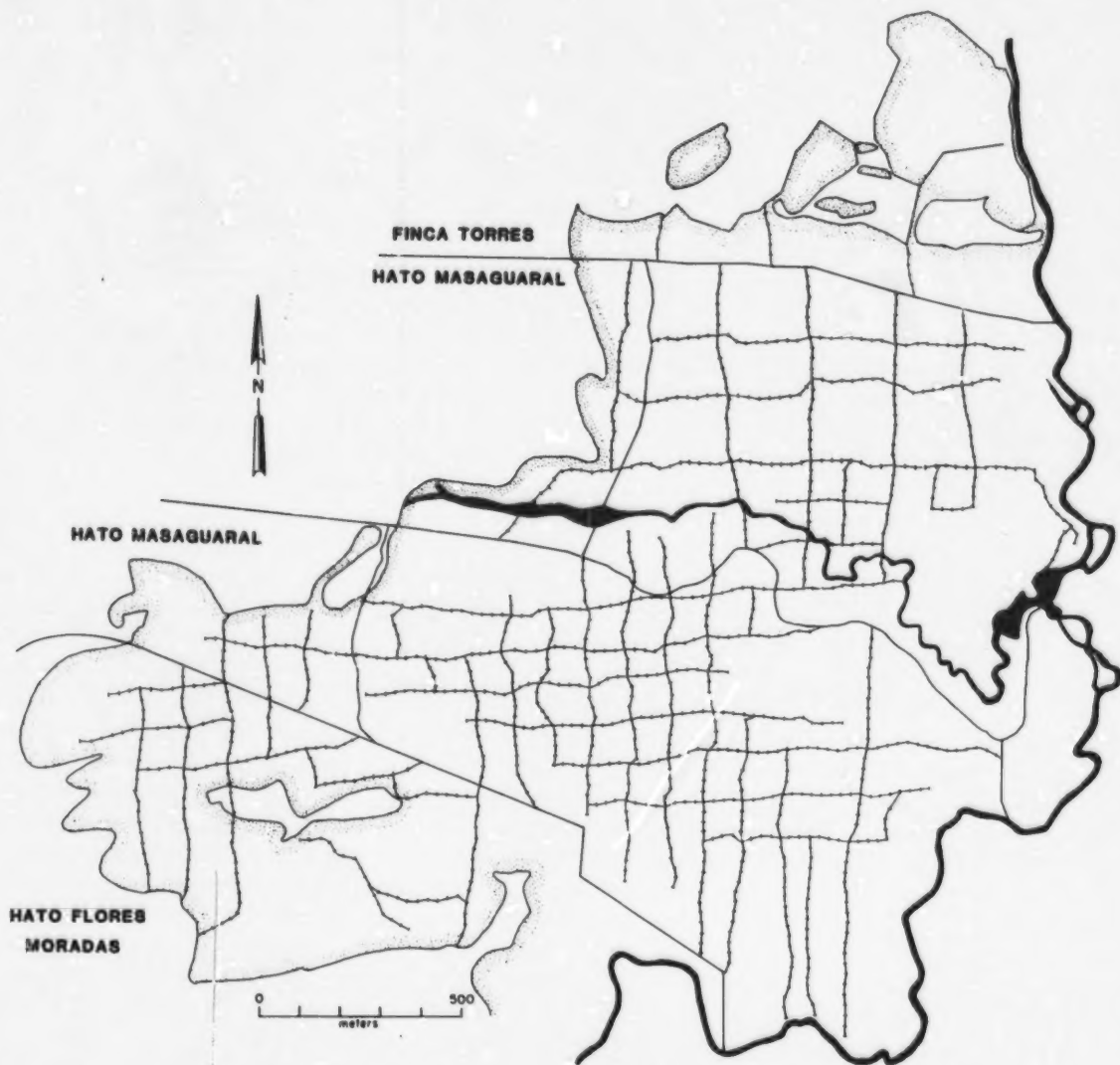


FIGURE 2.—Study area showing trail system. To the west the forest intergrades with savanna. To the east, it continues past the seasonal river, the Caño Caracol, for another 3 km or more. Marks on trails are 25 m apart. Trail grid covers three cattle ranches: Hato Masaguaral, Hato Flores Moradas, and Finca Torres.

part of the capuchin diet, and the 4 m requirement would have ignored many fruiting shrubs. All lianas, vines, and climbing trees were ignored. The total area sampled was 7.2 ha.

SPATIAL DISTRIBUTION.—The distribution in space of each tree species in the forest was measured by determining its abundance in a number

of identically-sized quadrats. I then used two indices, Morisita's index (I_d) and Rasmussen's index (RU), to measure the spatial pattern.

Spatially-defined quadrats 125 m² (25 × 5 m) or larger were distinguished by subdividing each transect line into 25 m sections. The pattern of spatial dispersion that is detected, however, de-

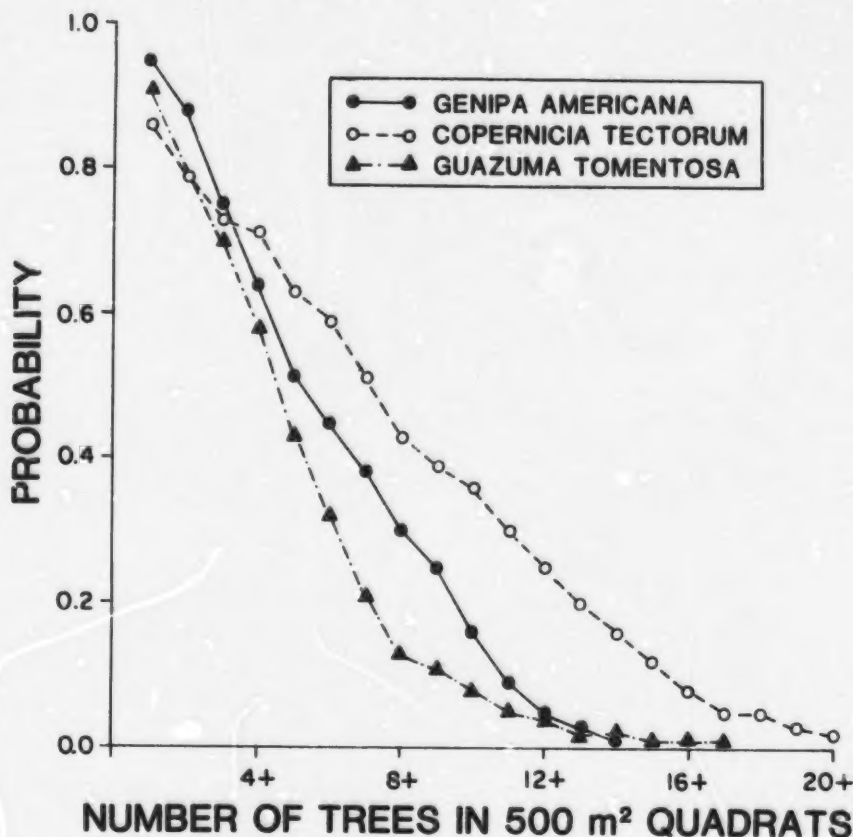


FIGURE 3.—The probability of recording n or more trees in 500 m² quadrats. Data plotted for the three most abundant trees.

depends on the quadrat size chosen. The lower limit was set by following Archibald's (1949) recommendation that most quadrats should contain at least one individual of at least one of the more common species. Figure 3 indicates that a quadrat area of 500 m² meets this requirement: the second and third most abundant tree species, *Genipa americana* and *Guazuma tomentosa*, occur at least once in over 90% of quadrats of this size. The most common species, the palm *Copernicia tectorum*, occurs in 86% of all quadrats. These 500 m² quadrats were derived by pooling four consecutive 25 m sections along the transect lines (4 × 25 × 5 m). The upper limit on quadrat size for estimates of spatial distribution is that a single quadrat must not intersect more than one of the

presumed local clumps of abundance (Poole, 1974). A quadrat area of 500 m² also meets this requirement.

Morisita's index (I_s) measures the extent to which each species is spatially clumped given the specified quadrat size (Poole, 1974):

$$I_s = \sum_{i=1}^N \frac{n_i(n_i - 1)}{n(n - 1)} N,$$

where N is the number of quadrats, n_i is the number of individuals in the i^{th} quadrat, and n is the total number of individuals in all quadrats. Deviation of the index from 1, which indicates a random distribution, can be tested using the F statistic.

Morisita's index provides a measure of the

consistency or *patchiness* in space of a particular species in the forest, or the extent to which individuals are nonrandomly distributed among quadrats. The index does not measure the spatial distribution of quadrats (the degree to which quadrats with high abundances of a particular species are clumped in space). Are these high frequency quadrats scattered throughout the forest or do they occur in specific locations? This *spread*, or its opposite, *clumping*, is built into another index, Rasmussen's index RU , originally developed to describe the spatial heterogeneity of baboon range use (Rasmussen, 1979; 1980). This index adds a measure of spread to the measure of consistency by weighting the effect of quadrat density by the distance between quadrats:

$$RU = \frac{\sum_{i=1}^N [(X_i - \bar{X})^2 / N]}{\bar{X}},$$

where X_i is the sum of individuals of a particular species in the i^{th} pair of quadrats divided by the distance between the centers of those quadrats, N is the total number of pairs of quadrats ($= N(N-1)/2 = 9,180$), and

$$\bar{X} = \frac{\sum_{i=1}^N X_i}{N}.$$

Like Morisita's index, this is not independent of quadrat size, and I continued to use the 500 m² quadrats.

To understand the relationship between these two indices, I compared I_d and RU values for 14 tree species commonly used by capuchins. Plotting the natural log of Morisita's index for these 14 species against Rasmussen's index yields a straight line (Figure 4), suggesting that proportionate changes in Morisita's index produce a linear response in Rasmussen's. The correlation between the two is high ($r = 0.99$), which indicates that most of the variance in the clumping of these 14 species is accounted for by the consistency of each species' distribution. Any remaining variance is the effect of spread. I derived a simple index of spread for each species by

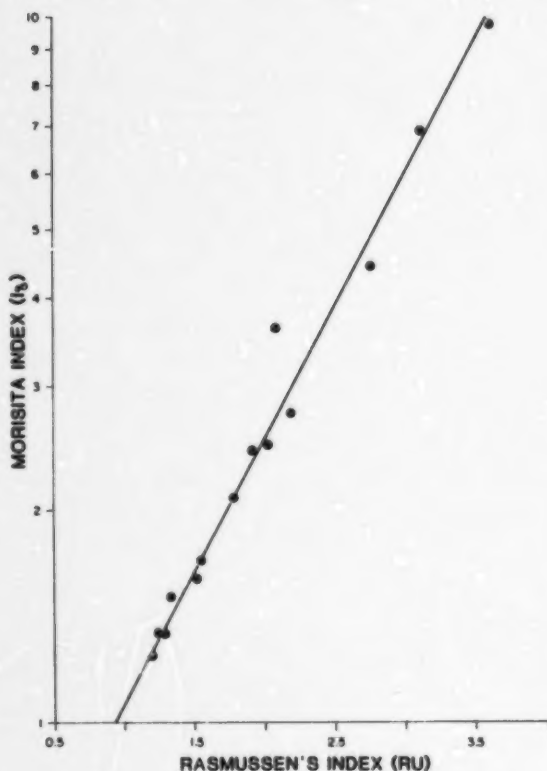


FIGURE 4.—Linear regression of Morisita's index (I_d) and Rasmussen's index (RU) for 14 tree species commonly used by capuchins. Morisita's index scaled logarithmically.

dividing the observed RU value by the expected. The validity of this index depends on the validity of the regression line between the two indices. The lower the value of the spread index, the more the quadrats of high abundance are spread out through the forest.

PHENOLOGY.—The temporal fluctuations in the availability of dried old leaves, mature and young leaves, leaf buds, ripe and unripe fruits, and flowers and flower buds were tabulated for 117 trees in 21 species. These species were chosen because they were common in the forest and because I suspected they were eaten by capuchins. Their phenological states were recorded between the fifth and tenth day of every month between November 1977 and December 1978. I examined each tree, and for each potential food

category (ripe fruits, young leaves, etc.) assigned an abundance score (none = 0, very few = 1, few = 2, some = 3, many = 4). These scores represented a subjective index of abundance. Abundance scores for all trees of a given species were averaged each month to provide a monthly abundance score. Monasterio and Sarmiento (1976) give an excellent overview of the phenological strategies of the tree species in this region.

BEHAVIORAL SAMPLING

Behavioral information is based primarily on a single group of capuchins, hereafter called the main group. Results were confirmed by less systematic observations on 11 other groups that were followed throughout the study. The main group was composed of a single adult male, two subadult males, from six to eight adult females and a number of juveniles and infants, a composition that is close to the population average for this area. Group size fluctuated around 20 animals during the study. By the start of systematic behavioral sampling, I could recognize each individual, and could approach to within two meters without disturbing the animals.

Fieldwork began in June 1977 and lasted until July 1979. I started systematic behavioral observations in November 1977, and for the next 14 months conducted five-day samples at the beginning of each month. Each day (0530–1830 hr) was divided into half-hour sample periods. I began recording as soon as it was light enough to recognize individuals. Sunrise was as early as 0610 hr in late May and early June, and as late as 0651 hr in late January and early February. Observations therefore normally began between 0545 and 0615 hr. Data collection ended when animals began entering their sleeping trees, which all group members did around the same time. The earliest sunsets (1808 hr) were in early November, and the latest (1854 hr) were in mid-January. The group tended to be at least in the vicinity of a sleeping tree at sunset.

DIET.—A number of different methods have been used to quantify primate diet (see Clutton-

Brock, 1977), and each estimates diet composition in a different way. Estimates of actual weight of matter consumed (e.g., Hladik and Hladik, 1969) probably provides the most reliable measure of diet composition, but this method requires excellent observation conditions and only small samples can be generated per unit effort. In addition, the relative bulk of an item ingested need not be correlated with its importance in the diet. Direct measurement of the proportion of time spent taking different food (e.g., Chivers, 1974; Clutton-Brock, 1975a; Waser, 1977) has the advantage that these data can be obtained for most species under most observation conditions. It cannot be directly compared with the "weight consumed" method because feeding rate varies among foods. Finally, one can measure the frequency with which an item is taken (e.g., Struhsaker, 1975; Oates, 1977; Rudran, 1978). Continuously recording new items taken will tend to overemphasize rare items and underemphasize common ones (Waser, 1977), but such sampling tends not to miss rare, potentially important food sources.

In this study I used the last two methods simultaneously. Using the frequency method I recorded every item ingested by an animal, if the item had not been ingested by the same animal in the preceding half hour. Considered items were: defined parts of specific plant species (see Table 6), identified invertebrates (see Table 7), or unidentified objects taken from a specific substrate or microhabitat (see Appendix II). The half hour limitation was necessary to distinguish records, but it was rarely invoked because capuchins have a high diet diversity and shift foraging behavior frequently. Using the time interval, I recorded the behavior of an individual the first time it was encountered during each half-hour sample period. Each record noted what food items were discovered or ingested during the first five seconds. This slow scan sample of the group gives an unbiased estimate of time feeding on each item (J. Altmann, 1974). In theory, the frequency method will overrepresent items consistently fed on for short periods of time. Thus,

with the capuchins, the proportion of invertebrates in the diet would be emphasized at the expense of fruits, and the proportion of different fruits would be biased toward species of small trees. In practice, I found little difference: with the time interval, of 4,283 records in which the item taken was identified, 61.6% were of plant origin; with the frequency method, the percentage was 62.3% (6,737 records). Estimates of the proportions of different fruits in the diet derived from the two methods were also very similar (Table 1). The frequency method was used to describe capuchin diet.

Results might also be biased if age-sex classes forage in different ways (Robinson, 1981), and if certain classes were sampled disproportionately more than their percent composition in the group. Based on 10,355 frequency records (including records in which no capture was made, and restricted to animals present during the full 14 months), however, the observed distribution of records among age-sex classes (Table 2) is not strongly different from the expected. Differences were statistically significant however ($p < 0.001$, χ^2 test) largely because the conspicuous adult male, who on average was positioned in the center of the group (Robinson, 1981), was recorded more than expected, and because young juveniles, who were still nursing through their first year, were foraging less than expected.

TIME BUDGETS.—During each half hour sample period I recorded the behavior of an individual the first time it was encountered. Behaviors were divided into eight broad categories: foraging, moving, resting, self-cleaning, grooming, playing, and other social and non-social behaviors. Each record noted, for the first behavior that lasted at least 5 seconds, the time, the identity of the individual, and the subject's activity. If the animal was foraging I described the technique used (27 foraging actions were defined: see Appendix I), the food item taken if any, and the substrate from which it was taken. For invertebrate foraging I noted whether a capture took place during the five seconds (a "capture" included discovery of an item and did not require

that the animal ingest the item). I judged the height at which the subject was found, estimating to within 1 m for heights up to 6 m, and to within 2 m for heights up to 20 m. The subject's position in the trees was also noted: supports greater than 15 mm in diameter (boughs), between 5–15 mm (branches), and less than 5 mm (twigs) were distinguished. I noted the distance to and identity of the nearest neighbor. Estimates of nearest-neighbor distance were placed into one of 11 categories (0, <1, 1, 2, 3, 4, 5, 6, 7–8, 9–10, >10 meters). Following this record I searched for another individual. Usually about 75% of the individuals in the group were sampled in the first 20 minutes of each period, none more than once.

From this modified slow scan sample of the study, the proportion of time in different activities can be calculated (J. Altmann, 1974). Because of the 20 minute duration of the scan however, the synchrony of activities among individuals cannot be estimated. The scan was further modified by noting only the first behavior of a subject animal that lasted at least five seconds, in order to avoid brief acts occurring while the animal was predominantly occupied in a different activity (Struhsaker, 1975). For unbiased estimates of time budgets, recording the subject's activity at first sighting (the first behavior sustained for about two seconds, Oates, 1977) is more appropriate. In practice this modification is minor because of the broad behavioral categories used in this study.

Unequal distributions of observations can introduce biases when comparing across months, a problem for which Altmann and Altmann (1970) and Post (1981) offer corrections. In the present study, sample sizes were large enough and the distribution of observation across months uniform enough to calculate time budgets directly, by summing records in each category.

MOVEMENTS AND USE OF SPACE

Description of group movements requires accurate maps. Maps of the study area were pro-

TABLE 1.—Comparison of diet sampling techniques using ripe fruit results.

Species	Frequency item taken		Time spent taking item	
	No. of records	%	No. of records	%
<i>Ficus pertusa</i>	827	25.5	582	29.1
<i>Guazuma tomentosa</i>	508	15.7	348	17.4
<i>Genipa americana</i>	257	7.9	116	5.8
<i>Randia hebecarpa</i>	250	7.7	155	7.7
<i>Cordia collococca</i>	182	5.6	101	5.0
<i>Ficus trigonata</i>	180	5.6	119	5.9
<i>Annona jahnii</i>	136	4.2	86	4.3
<i>Vitex orinocensis</i>	124	3.8	83	4.2
<i>Zanthoxylum culantrillo</i>	107	3.3	51	2.6
<i>Paullinia cururu</i>	87	2.7	57	2.8
<i>Psychotria anceps</i>	76	2.3	24	1.2
<i>Ficus</i> sp.	74	2.3	37	1.8
<i>Diospyros terensis</i>	63	1.9	39	1.9
<i>Guettarda divaricata</i>	54	1.7	43	2.1
<i>Melothria trilobata</i>	34	1.0	21	1.0
<i>Coccoloba caracasana</i>	34	1.0	16	0.8
<i>Copaifera officinalis</i>	32	1.0	11	0.5
<i>Sterculia apetala</i>	24	0.7	6	0.3
<i>Vitex compressa</i>	20	0.6	16	0.8
<i>Cissus sicyoides</i>	19	0.6	7	0.3
<i>Passiflora serrulata</i>	16	0.5	11	0.5
<i>Capparis coccolobifolia</i>	15	0.5	8	0.4
<i>Chlorophora tinctoria</i>	11	0.3	9	0.4
<i>Copernicia tectorum</i>	8	0.2	7	0.3
<i>Cecropia</i> sp.	7	0.2	5	0.2
<i>Vitex capitata</i>	7	0.2	3	0.1
<i>Margaritaria nobilis</i>	6	0.2	3	0.1
<i>Phoradendron</i> sp.	6	0.2	3	0.1
<i>Randia venezuelensis</i>	6	0.2	2	0.1
<i>Spondias mombin</i>	5	0.2	1	0.05
<i>Bromelia chrysantha</i>	4	0.1	2	0.1
<i>Hecastostemon completus</i>	4	0.1	3	0.1
<i>Allophylus occidentalis</i>	4	0.1	3	0.1
<i>Cissus alata</i>	4	0.1	3	0.1
<i>Pithecellobium saman</i>	3	0.1	1	0.05
<i>Cordia polycephala</i>	3	0.1	1	0.05
<i>Tetracera volubilis</i>	3	0.1	—	—
<i>Hylocereus polyrhizus</i>	3	0.1	—	—
<i>Pithecellobium guaricense</i>	2	0.06	1	0.05
<i>Connarus venezuelanus</i>	2	0.06	—	—
<i>Malpighia emarginata</i>	2	0.06	—	—
<i>Hymenaea courbaril</i>	1	0.03	1	0.05
<i>Capparis odoratissima</i>	1	0.03	—	—
<i>Ouratea guildingii</i>	1	0.03	—	—
<i>Chomelia spinosa</i>	1	0.03	—	—
Totals	3239		2001	

TABLE 2.—Frequency of foraging records in different age-sex classes. Expected values are calculated from age-sex class composition of the group.

Parameters	Adult male	Adult females	Subadult males	Older juveniles	Younger juveniles
Observed	924	4672	932	3000	827
Expected	575	4603	1151	2877	1151

duced by surveying the extensive trail system (Figure 2). Trails in this north-south/east-west grid totalled over 60 km in length, and intersected one another at 50, 100, or 200 m intervals. Plastic flagging and marked aluminum strips were placed every 25 m along trails, and bearings between consecutive flags were taken using a Brunton pocket-transit. Errors of closure (Brinker, 1969) when drawing maps were always less than 5%.

Movements of the study group during the five-day sample period at the beginning of each month were plotted on these maps. Complete day movements, from dawn to dusk were recorded on 72 such days, and partial day movements were recorded on an additional 27. The center of mass of the group (see Altmann and Altmann, 1970; Waser and Floody, 1974) was estimated every half-hour beginning at 0530 hr. I assumed that the distance moved by the group in each half-hour period equalled the straight line distance between consecutive locations of the center of mass, and I calculated the turning angle between each pair of steps (see Figure 18; angle not calculated or included in summary statistics if the group did not move). In addition to describing these parameters of the group's movement, I also examined the resulting pattern of movement and noted the number of times that the group recrossed its own path on each day.

Use of space was also calculated for these 99 days. Every half hour I plotted the location of all individuals that could be found in a five-minute period. A line joining the outermost individuals formed an irregular polygon and defined the group spread. A taut line around consecutive half-hour group-spread polygons then formed an

irregular ellipse, and defined the group's occupancy of space for that half hour period.

To quantify the distribution of use of the home range, I superimposed a grid of 25×25 m quadrats ($\frac{1}{4}$ ha) on this map. All quadrats that were at least half inside each half-hour ellipse were noted. Scores therefore represent the number of half-hour samples in which each quadrat was occupied by at least one individual.

The quadrat size chosen influences both the estimate of the total home range area, and the resolution of differential use of that area (Rudran, 1978; Whitten, 1982). Using a quadrat size of $\frac{1}{4}$ ha generated a home range of 208.25 ha for the duration of the study. A quadrat size of 1 ha generated a range of 257 ha, an increase of 25%, and a 4 ha quadrat size produced a range of 328 ha. Accuracy of measurement is not determined by the choice of quadrat size. Smaller quadrat sizes will always generate smaller home ranges and finer resolution, but they are not necessarily more accurate. The group's use of space is only sampled for a limited period each month, and the positions of all individuals are not located at all times. One relatively subjective criterion for choosing an appropriate quadrat size is that it should be large enough to include all the area that a group probably used during the time frame of interest, but small enough to exclude areas that the group probably did not use. In this study I collapsed four $\frac{1}{4}$ ha quadrats to form a single 1 ha quadrat. In addition to meeting the above criterion, it allowed me to compare the group's use of space to the distribution of plant resources, which was also analyzed at this resolution, and gave me a more manageable number of quadrats (257 versus 833).

Results

ABUNDANCE AND DISTRIBUTION OF RESOURCES

RELATIVE DENSITY.—Along the 14.4 km of transects, in the total sample area of 7.2 ha, I recorded 9,427 individual trees of 84 species in 33 families (Table 3). The palm *Copernicia tectorum* was the most abundant species, but it was not found on the alluvial *medano* sand ridges. *Guazuma tomentosa* and *Genipa americana* were common and broadly distributed. The most fully represented plant family was the Fabaceae. Trees of species in both the Moraceae and the Rubiaceae were also common. Species richness of trees is similar to the Costa Rican dry forest described by Hubbell (1979).

SPATIAL DISTRIBUTION.—The spatial distribution of tree species in the *llanos* has been correlated with the extent of flooding during the wet season and the soil type (Taylor, 1978; Troth, in prep.), two characteristics that are not independent. Table 4 presents surface soil composition for three locations in the forest. The loamy sands, which never flood, are elevated alluvial deposits, continuous with the sandy *medano* (Troth Ovrebo, 1979) of the open savanna. These areas support a distinct flora, with the canopy dominated by *Vitex orinocensis* and the shrub layer by *Randia hebecarpa*. The loam sample was taken from an area that is frequently inundated during the wet season, and the clay sample from an area that is invariably so. It is these edaphic variations that result in the heterogeneous distribution of tree species.

Distribution maps for four tree species are shown in Figures 5 and 6. These maps were constructed by extrapolating from the relative densities in the 500 m² sample quadrats. *Randia hebecarpa* is the dominant understory shrub on the sand deposits. Some individuals also occur in other dry areas. *Pterocarpus acapulcensis*, a canopy tree, predominates in dry loam and clay areas that are not flooded for more than a couple of weeks at a time. The ubiquitous palm *Copernicia tectorum* tolerates extensive flooding, but appar-

ently not throughout the entire wet season (Troth Ovrebo, in prep.), and it is also infrequent on the dry sand areas. *Guazuma tomentosa*, a common medium-sized tree, has a wide tolerance and is found in both drier and wetter areas than the palm.

Table 3 indicates that most tree species in the forest are patchily distributed in space ($p < 0.001$, F test for deviation of Morisita's index from 1). I did not statistically test the deviation for the less common species, defined as those whose total abundance in the sample did not exceed 9. Table 5 compares Rasmussen's and Morisita's indices of patchiness and clumping for the 14 tree species most used by capuchins, and derives values for the spread index (SI). As examples: *Guettarda divaricata* is a species with high inconsistency (trees are patchily distributed in space) but also high spread (groups of trees are scattered through the forest rather than occurring in just a few locations). *Randia hebecarpa* is also highly inconsistent, but the quadrats with many individuals are clumped in only a few locations (primarily on sands). At the other extreme, *Guazuma tomentosa* is relatively consistent and the inconsistency that does exist is spread throughout the forest, while *Genipa americana* also has little spatial variation in abundance, but areas of high abundance are clumped.

SEASONAL VARIATION.—Of the 20 most abundant tree species in the forest, five species of the family Fabaceae (= Leguminosae) and *Cochlospermum vitifolium*, had dry deshiscent fruit not taken by capuchins, and two had relatively dry fruit only rarely taken. Eight of the remaining 12 species were among the 12 fruits that were taken most frequently. To illustrate the annual variation in fruit available to capuchins, I plotted the number of these 12 most frequently eaten species that had ripe fruit in each month of the study (Figure 7). There are species fruiting throughout the year, but fewer do so during the dry season. Average monthly rainfall for 1978 was significantly correlated with the number of tree species in fruit ($r_s = 0.56$, $p < 0.05$). Of the species that do fruit at this time, *Guazuma tomen-*

TABLE 3.—Abundance of trees over 4 m tall in sample area of 7.2 ha and the degree of clumping of each species using Morisita's index (I_d). If the calculated value is significantly different from I_d using the F-test, the conclusion is that the species is aggregated in space.

Taxon	Common name	Abundance	Morisita's I_d	F-test (p)
ANACARDIACEAE				
<i>Spondias mombin</i> L.	Jobo	142	1.30	ns
ANNONACEAE				
<i>Annona jahnii</i> Safford	Manirito	138	3.63	<0.001
<i>Duguetia riberensis</i> Aristeguieta	Annoncillo	2	—	—
APOCYNACEAE				
<i>Himatanthus articulatus</i> (Vahl) Woodson	Mijao	1	—	—
ARECACEAE				
<i>Copernicia tectorum</i> (H.B.K.) Mart.	Palma llanera	1095	1.51	<0.001
BIGNONIACEAE				
<i>Godmania aesculifolia</i> (H.B.K.) Standley	Cornicabro	4	—	—
<i>Jacaranda obtusifolia</i> Humboldt and Bonpland	Flor morada	109	7.49	<0.001
<i>Tabebuia billbergii</i> (Burman and K. Schumann) Standley	Flor amarillo	1	—	—
<i>Tabebuia chrysantha</i> (Jacquin) Nichols sensu lato	Flor amarillo	8	—	—
BOMBACACEAE				
<i>Bombacopsis quinata</i> (Jacquin) Dugand	Cedro dulce	12	4.42	ns
<i>Ceiba pentandra</i> (L.) Gaertner	Ceiba	2	—	—
BORAGINACEAE				
<i>Cordia alliodora</i> L.	Cuajaro	254	1.60	<0.001
CACTACEAE				
<i>Cereus hexagonus</i> (L.) P. Miller	Cardon	3	—	—
<i>Pereskia guamacho</i> Weber	Guamacho	19	33.30	<0.001
CAPPARIDACEAE				
<i>Capparis coccolobifolia</i> Martius	Rabo pelado	74	6.74	<0.001
<i>Capparis odoratissima</i> Jacquin	Olivo	16	1.99	<0.001
<i>Crataeva tapia</i> L.	Toco	1	—	—
COCHLOSPERMACEAE				
<i>Cochlospermum vitifolium</i> (Willdenow) Sprengel	Carneval	163	2.07	<0.001
CONNARACEAE				
<i>Connarus venezuelanus</i> Baillon	Conchagruesa	5	—	—
DILLENIACEAE				
<i>Curatella americana</i> L.	Chaparro bobo	5	—	—
EBENACEAE				
<i>Diospyros ierensis</i> Britton	Cacaito	152	2.42	<0.001
ERYTHROXYLACEAE				
<i>Erythroxylum hondense</i> H.B.K.	Jayito	6	—	—
EUPHORBIACEAE				
<i>Margaritaria nobilis</i> L.f.	Zarcillo	246	6.74	<0.001
<i>Sapium aucuparium</i> Jacquin	Lechero	45	1.18	ns
Unknown species	Asta blanca	1	—	—
FABACEAE (CAESALPINIOIDEAE)				
<i>Caesalpinia coriaria</i> (Jacquin) Willdenow	Divedive	345	1.73	<0.001
<i>Copaifera officinalis</i> H.B.K.	Aceite	10	3.24	ns
<i>Hymenaea courbaril</i> L.	Algorrobo	11	7.96	<0.001
<i>Sclerolobium guianense</i> Benth	Cacho hediondo	2	—	—
FABACEAE (MIMOSOIDEAE)				
<i>Acacia articulata</i> Ducke	Uña de gavilan	77	6.49	<0.001
<i>Albizia cf. caribaea</i> (Urban) Britton and Rose	Caro, Carabali	34	1.82	ns

TABLE 3.—Continued.

Taxon	Common name	Abundance	Morisita's J_h	F-test (p)
<i>Albizia guachapele</i> (H.B.K.) Dugand	Masaguaro	5	—	—
<i>Enterolobium cyclocarpum</i> (Jacquin) Grisebach	Caracara	34	1.30	ns
<i>Pithecellobium daulense</i> Spruce ex Benth	Veramacho	302	1.44	<0.001
<i>Pithecellobium guaricense</i> Pittier	Orore	44	4.01	<0.001
<i>Pithecellobium ligustrinum</i> (Jacquin) Klotzsch	Taguapire	9	—	—
<i>Pithecellobium saman</i> (Jacquin) Benth	Saman	17	2.15	ns
<i>Pithecellobium tortum</i> Martius	Quiebrahacho	589 ^a	1.76	<0.001
FABACEAE (FABOIDEAE)				
<i>Erythrina velutina</i> Willdenow	Bucare	1	—	—
<i>Lonchocarpus crucisrubrae</i> Pittier, vel. sp. aff.	Menuito	334	—	—
<i>Lonchocarpus hondurensis</i> Benth, vel. sp. aff.	Tocorito	8 ^b	—	—
<i>Lonchocarpus</i> aff. <i>pictus</i> Pittier	Majomo negro	122	3.03	<0.001
<i>Machaerium dubium</i> (H.B.K.) Rudd	Almendron	73	8.83	<0.001
<i>Platymiscium pinnatum</i> (Jacquin) Dugand	Roble	34	9.89	<0.001
<i>Pterocarpus acapulcensis</i> Rose	Drago	416	1.99	<0.001
FLACOURTIACEAE				
<i>Casearia mollis</i> H.B.K.	Tapacondi	32	5.30	<0.001
<i>Hecastostemon completus</i> (Jacquin) Sleumer	Barote	318	1.67	<0.001
LECYTHIDACEAE				
<i>Lecythis ollaria</i> Leofling	Coco de mono	1	—	—
MALPIGHIACEAE				
<i>Brysonima crassifolia</i> (L.) H.B.K.	Chaparro manteco	1	—	—
<i>Malpighia emarginata</i> DC.	Cerezo	19	11.95	<0.001
MELIACEAE				
<i>Trichilia trifolia</i> L. subsp. <i>trifolia</i>	Coloraito	157	1.93	<0.001
MORACEAE				
<i>Cecropia</i> sp.	Yagrumo	6	—	—
<i>Chlorophora tinctoria</i> (L.) Gaudichaud	Mora blanca	13	13.10	<0.001
<i>Ficus pertusa</i> L.f.	Matapalo	175	1.75	<0.001
<i>Ficus trigonata</i> L.	Higuerote	91 ^c	2.75	<0.001
<i>Sorocea sprucei</i> (Baillon) Macbride	Charro	48	17.21	<0.001
MYRTACEAE				
<i>Pseudonamomis umbellulifera</i> (H.B.K.) Kausel	Guayavito de agua	7	—	—
<i>Pseudonamomis</i> aff. <i>umbellulifera</i> (H.B.K.) Kausel	Cacho	61	9.10	<0.001
<i>Psidium guineense</i> Swartz	Guayavito	1	—	—
NYCTAGINACEAE				
<i>Guapira pacurero</i> (H.B.K.) Little	Guacharaco	1	—	—
<i>Neea spruceana</i> Heimerl.	Casavito	39	1.97	ns
OCHNACEAE				
<i>Ouratea guildingii</i> (Planchon) Urban	Casco de burro	47	2.84	<0.001
POLYGONACEAE				
<i>Coccoloba caracasana</i> Meisner	Uvero	96	2.47	<0.001
<i>Coccoloba ovata</i> Benth	Uverito de agua	6	—	—
<i>Ruprechtia coriacea</i> (Karsten) Blake	Canoito	45	5.16	<0.001
<i>Ruprechtia ramiflora</i> (O. Kuntze) Meyer	Palo de agua	3	—	—
RHAMNACEAE				
<i>Zizyphus saeri</i> Pittier ^a	Limoncillo	33	8.30	<0.001
ROSACEAE				
<i>Licania apetala</i> (E. Meyer) Fritsch	Mamoncillo	1	—	—

TABLE 3.—Continued.

Taxon	Common name	Abundance	Morisita's I_i	F-test (p)
RUBIACEAE				
<i>Chomefia spinosa</i> Jacquin	Espinito	67	6.14	<0.001
<i>Genipa americana</i> L. var. <i>caruto</i> (H.B.K.) K. Schumann	Caruto	797	1.24	<0.001
<i>Guettarda divaricata</i> (Humboldt and Bonpland ex Roemer and Schultes) Standley	Punteral	77	6.89	<0.001
<i>Psychotria anceps</i> H.B.K.	Agallon	(364) ^d	2.07	<0.001
<i>Randia hebecarpa</i> Bentham	Cachito	(430) ^d	4.47	<0.001
<i>Randia venezuelensis</i> Steyermark	Diente de perro	69	4.29	<0.001
RUTACEAE				
<i>Zanthoxylum caribaeum</i> Lamarck	Mapurito	14	6.42	<0.001
<i>Zanthoxylum culantrillo</i> H.B.K.	Bosu	516	1.33	<0.001
SAPINDACEAE				
<i>Allophylus cobbe</i> Leenhouts	Pata de danta	66	9.73	<0.001
<i>Cupania</i> sp.	Zapatero	11	42.57	<0.001
SOLANACEAE				
<i>Cestrum latifolium</i> Lamarck	Juan de la calle	5	—	—
STERCULIACEAE				
<i>Guazuma tomentosa</i> H.B.K.	Guacimo	648	1.33	<0.001
<i>Sterculia apetala</i> (Jacquini) Karsten	Camoruco	17	3.22	ns
VERBENACEAE				
<i>Vitex compressa</i> Turczaninow	Guarataro aceituno	98	4.33	<0.001
<i>Vitex orinocensis</i> H.B.K.	Guarataro pardillo	1 ^e	—	—
<i>Vitex orinocensis</i> var. <i>multiflora</i> (Miguel) Huber, vel. sp. aff.	Guarataro pardillo	75 ^f	9.79	<0.001
Total		9427		

^a Probably includes trees of *Pithecellobium carabobense* Harms.^b May include trees of *Lonchocarpus minimiflorus* Donn. Smith.^c Probably includes a second species, *Ficus* aff. *trigonata* L.^d These shrub species were counted if "trees" were over 2 m tall.^e May be a tree of *Vitex capitata* Vahl.^f May include trees of *Vitex appunii* Moldenke.

TABLE 4.—Surface soil characteristics in three sample plots (data from R.G. Troth Ovrebo).

Soil classification	% Sand	% Silt	% Clay	pH	Standing water
Loamy sand	84.2	8.6	7.2	4.85	never
Loam	22.8	38.0	39.2	4.15	frequent during wet season
Clay	20.2	37.6	42.2	3.85	always during wet season

tosa, the most important, has small, hard, dry fruits that were not preferred when other species come into fruit. *Ficus pertusa* fruits in every month, but only a few individuals produce fruit during the dry season. With the approach and

onset of the rains there is a peak in fruit abundance, followed by another peak late in the wet season (for a similar phenological pattern see Snow and Snow, 1964; Foster, 1973).

Fruit abundance varies considerably among

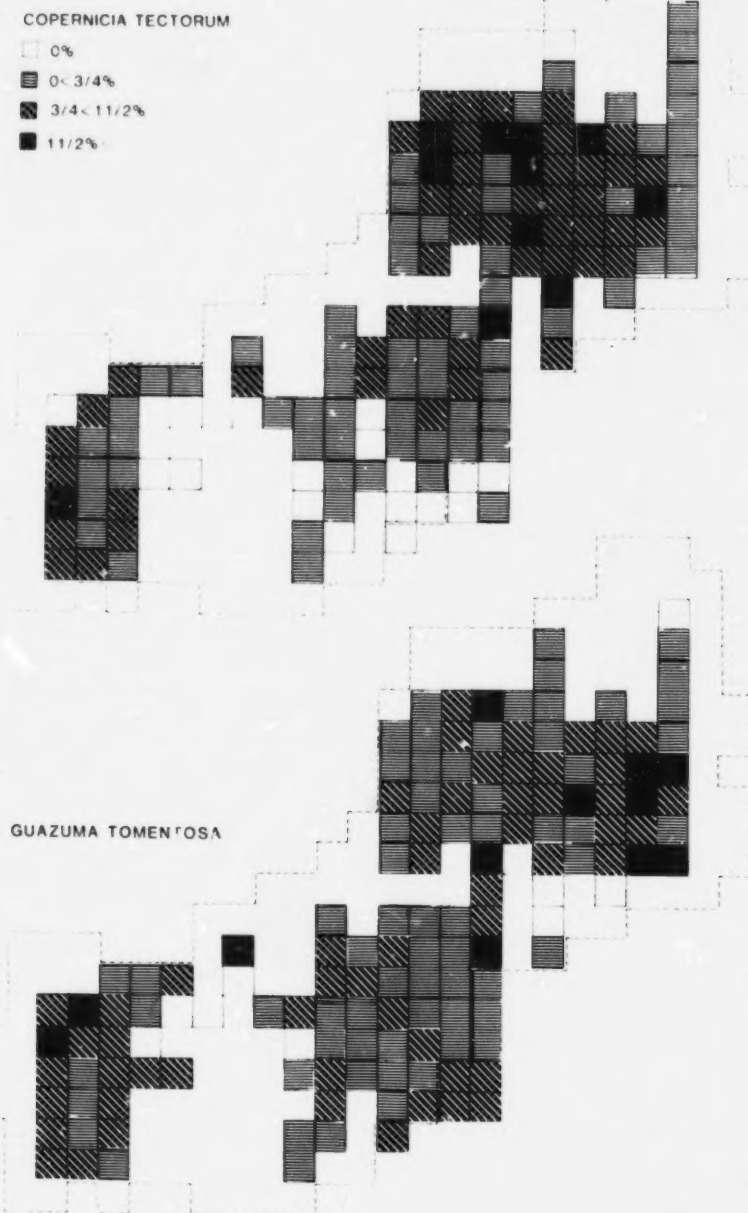


FIGURE 5.—Spatial distribution of *Copernicia tectorum* and *Guazuma tomentosa* trees. Percentage of trees in each sampled quadrat indicated.

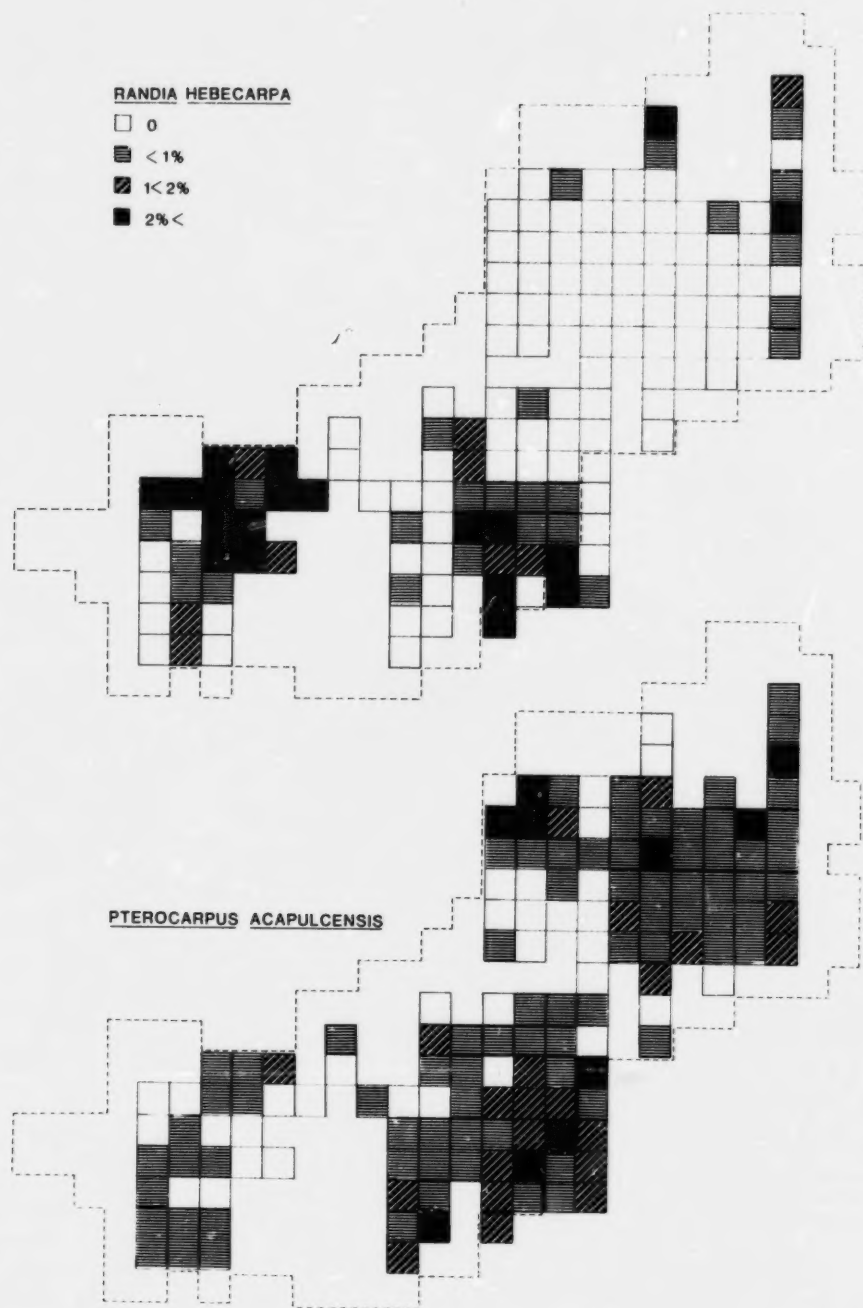


FIGURE 6.—Spatial distribution of *Randia hebecarpa* and *Pterocarpus acapulcensis* trees. Percentage of trees in each sampled quadrat indicated. Dotted line circumscribes the 257 ha range of the main study group.

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TABLE 5.—Clumping of the 14 tree species most used by *Cebus olivaceus*.

Species	Rasmussen's clumping index (RU)	Rank	Morita's index (I_d)	Rank	Spread index (SI)	Rank
<i>Vitex orinocensis</i>	3.520	1	9.79	1	1.021	9
<i>Guettarda divaricata</i>	3.107	2	6.89	2	0.989	4
<i>Randia hebecarpa</i>	2.772	3	4.47	3	1.048	14
<i>Ficus trigonata</i>	2.129	4	2.75	5	1.020	8
<i>Annona jahnii</i>	2.076	5	3.63	4	0.863	1
<i>Coccoloba caracasana</i>	2.024	6	2.47	6	1.031	13
<i>Diospyros ierensis</i>	1.962	7	2.42	7	1.011	6
<i>Psychotria anceps</i>	1.783	8	2.07	8	1.012	7
<i>Ficus pertusa</i>	1.546	9	1.75	9	0.985	3
<i>Cordia alliodora</i>	1.510	10	1.60	10	1.030	12
<i>Copernicia tectorum</i>	1.329	11	1.51	11	0.950	2
<i>Zanthoxylum culantrillo</i>	1.285	12	1.33	12	1.025	10
<i>Guazuma tomentosa</i>	1.251	13	1.33	13	0.998	5
<i>Genipa americana</i>	1.208	14	1.24	14	1.030	11

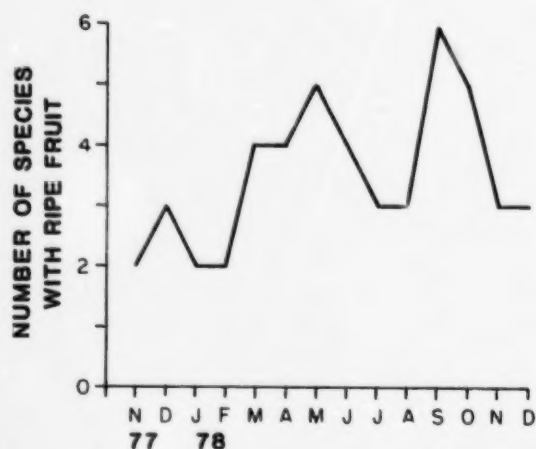


FIGURE 7.—Fruits available to capuchins through the year, measured by number of species carrying ripe fruit in each month.

different years. Following the extremely dry year of 1977, 1978 was characterized by a failure of the *Copaifera officinalis* crop in the dry season, and failures of the *Hecastostemon completus* and *Spondias mombin* crops at the beginning of the wet. These three species have constituted a large

part of the capuchin diet in recent years. In 1978 however, the *Annona jahnii* fruit production was high. Such fluctuations in fruit abundance across years have been reported before in tropical forests (Foster, 1977; Foster, 1980; Leigh et al., 1983).

Seasonal variation in invertebrate abundance does not show the same pattern as that of fruits (Wolda, 1978, 1979). During the dry season, the abundance of many leaf litter invertebrates, such as tettigoniid grasshoppers, appears to be higher, and might reflect migration from drier grassland into the moister forest (see Janzen, 1973). In the trees and shrubs however, phytophagous insects are virtually absent, because with little standing water and low soil moisture, plant productivity is low (see Janzen, 1973; Buskirk and Buskirk, 1976) and many trees and shrubs drop their leaves. The onset of the rains, the time of which varies considerably from year to year, triggers a leaf flush, and a peak in the caterpillar abundance. During the wet season, much of the gallery forest, with the exception of the sandy ridges, has standing water. This effectively eliminates the forest floor as a foraging microhabitat during this season.

DIET

Of the 7,683 feeding records taken during the study, 4,200 were items of plant origin (55% of diet) from 13 vine, 3 herb, 4 shrub, 38 tree, 2 grass, and 6 epiphyte species; 1,422 were identified animals, mainly invertebrates; 1,115 were unidentified invertebrates (animal material totalled 33% of the diet); 496 were items of unknown origin; 3 were regurgitated matter; and 447 were records in which the animal was drinking. Most of the drinking records were in the dry season.

VEGETATIVE MATERIAL.—In 53 of 67 observations of capuchins uprooting saplings and eating the roots, the plant was identified as *Cochlospermum vitifolium*. This action, performed mainly by the larger males, uprooted saplings one to two meters high, with main tap roots 20 cm long and 5 cm in diameter at ground level. Smaller animals attempted, but rarely succeeded in this activity. Roots were entirely eaten and probably provide an important nutrient source at the height of the dry season when overall food availability is low.

Only 6% (497 records) of feeding observations involved buds, leaves, or shoots (Table 6). The majority (85%) of these were cases in which the animal masticated the item, presumably largely for its water content, and spat out the fibrous material. This was especially common in the dry season and involved the leaves of *Oncidium* orchids and the rachis pith of *Copernicia* palm fronds. To reach the pith, capuchins would break open the rachis of the frond, using both their hands and teeth, and remove a section of pith. *Copernicia* frond buds were pulled out when they first appeared in the crown and actually were ingested. Young leaves and buds of trees in the family Fabaceae were also eaten.

FLOWERS AND FRUITS.—Flowers were rarely taken, and then usually opportunistically. The one exception were the large flowers of the epiphytic cactus *Hylocereus polyrhizus*, which animals not only searched out, but which were also the objects of competition.

Fruits constituted the largest (46%) category

of food items. At least 50 species from 30 families were taken, although two families, the Moraceae and the Rubiaceae, were overrepresented (50% of fruit records) both in number of feeding observations and in the number of species involved. Figs, represented at the study site by the small fruited *Ficus pertusa* and by the large fruited *F. trigonata*, were the items taken most frequently. *F. pertusa* fruited very asynchronously and was a staple almost every month of the year. Their trees carried a large crop and were frequently the first visited in the morning (Robinson, 1985a).

Like the figs, most fruits eaten by capuchins were fleshy. If they contained large seeds, as in *Cordia collococca*, *Diospyros ierensis*, and the *Vitex* species, these were often not ingested. If the seeds were swallowed, they tended to pass intact through the gut, with the exception of *Coccoloba caracasana* and *Zanthoxylum culantrillo*, whose seeds were crushed with the teeth and presumably provided nutrients to the animals. Seeds of the sedge *Scleria setulosa-ciliata* and the grass *Lacisis anomala* were taken on occasion.

Capuchins frequently monitored the ripeness of fruits by squeezing and biting into them. This was especially common with *Genipa americana*, whose ripe and unripe fruits are difficult to distinguish. Unlike the diet of the sympatric red howler monkey *Alouatta seniculus* (Rudran, Crockett, pers. comm.) almost all fruits eaten by the capuchins were ripe, through frequently only barely so. The notable exception was the unripe fruit of the palm *Copernicia*. The whole fruit was taken at the height of the dry season, in March and April, when the palm stone was still relatively soft. Other unripe fruits taken include those of *Marsdenia undulata*, before the seed and parachuting devices hardened, and *Centrosema pubescens* before the pods dried. Hard fruits such as *Sterculia apetala* and *Hymenaea courbaril* were pounded open by the animals (see also Struhsaker and Leland, 1977; Izawa and Mizuno, 1977; Terborgh, 1983), or cracked open with their teeth. Juveniles often were unable to open these fruits.

TABLE 6.—Use of different plant species based on frequency records.

Taxon	Flowers			Fruits			Leaves			Shoots		Roots	Resin	Unknown	Total
	Buds	Mature	Age un- known	Unripe	Ripe	Seeds	Buds	Young	Mature	Young	Flowers				
AMARYLLIDACEAE															
<i>Hymenocallis venezuelensis</i>										1		1			2
ANACARDIACEAE															
<i>Spondias mombin</i>					5						1				6
ANNONACEAE															
<i>Annona jahnii</i>				4	136										140
ARECACEAE															
<i>Copernicia tectorum</i>	5			181	8	5 ^a	38		368 ^b	1					606
ASCLEPIADACEAE															
<i>Marsdenia undulata</i>				21											21
BIGNONIACEAE															
<i>Macfadyena uncata</i>		1													1
BORAGINACEAE															
<i>Cordia collococca</i>				5	182										187
<i>Cordia polycephala</i>					3										3
BROMELIACEAE															
<i>Bromelia chrysantha</i>		3		2	4			1	1						11
<i>Bromelia plumieri</i>				4											4
CACTACEAE															
<i>Hylocereus polyrhizus</i>		4			3				2						9
CAPPARACEAE															
<i>Capparis coccolobifolia</i>	4	3			2	15									24
<i>Capparis odoratissima</i>					1										1
COCHLOSPERMACEAE															
<i>Cochlospermum vitifolium</i>															53
COMBRETACEAE															
<i>Combretum fruticosum</i>	4														4
CONNARACEAE															
<i>Connarus venezuelanus</i>				2	2										4
CUCURBITACEAE															
<i>Luffa operculata</i>				1											1
<i>Melothria trilobata</i>					34										34
CYPERACEAE															
<i>Scleria setuloso-ciliata</i>						18									18
DILLENIACEAE															
<i>Tetracera volubilis</i>	2				3										5
EBENACEAE															
<i>Diospyros ierensis</i>				2	63										65
EUPHORBIACEAE															
<i>Dalechampia scandens</i>						1									1
<i>Margaritaria nobilis</i>					6										6
FABACEAE (CAESALPINOIDEAE)															
<i>Copaifera officinalis</i>					32										32
<i>Hymenaea courbaril</i>					1										1
FABACEAE (MIMOSOIDEAE)															
<i>Albizia guachapele</i>							3								3
<i>Entada polystachya</i>							2								2

TABLE 6.—Continued.

Taxon	Flowers			Fruits			Leaves			Shoots		Roots	Resin	Unknown	Total
	Buds	Mature	Age un- known	Unripe	Ripe	Seeds	Buds	Young	Mature	Young	Flowers				
<i>Pithecellobium daulense</i>									2				8		10
<i>Pithecellobium guaricense</i>					2										2
<i>Pithecellobium sawan</i>					3										3
FABACEAE (FABOIDEAE)															
<i>Centrosema pubescens</i>		2		3											5
<i>Machaerium moritzianum</i>							1	10	1						12
FLACOURTIACEAE															
<i>Hecastostemon completus</i>				1	4										5
GRAMINAE															
<i>Lacisis anomala</i>						5			2						7
LORANTHACEAE															
<i>Phoradendron</i> sp.					6										6
MALPIGHIACEAE															
<i>Malpighia emarginata</i>					2										2
MALVACEAE															
<i>Wissadula periplocifolia</i>						8									8
MARANTACEAE															
<i>Thalia geniculata</i>		2				2									4
MELIACEAE															
<i>Trichilia trifolia</i>			1												1
MORACEAE															
<i>Cecropia</i> sp.					7										7
<i>Chlorophora tinctoria</i>					11										11
<i>Ficus pertusa</i>				6	827										833
<i>Ficus trigonata</i>				19	180										199
<i>Ficus</i> sp.				14	74										88
OCHNACEAE															
<i>Ouratea guildingii</i>					1										1
ORCHIDACEAE															
<i>Oncidium carthaginense</i>									2						2
<i>Oncidium cebolleta</i>		4							51						55
PASSIFLORACEAE															
<i>Passiflora serrulata</i>					16										16
POLYGONACEAE															
<i>Coccoloba caracasana</i>				28	34										62
ROSACEAE															
<i>Licania apetala</i>				1											1
RUBIACEAE															
<i>Chomelia spinosa</i>					1										1
<i>Genipa americana</i>			1	3	257										261
<i>Guettarda divaricata</i>					54										54
<i>Psychotria anceps</i>					76										76
<i>Randia hebecarpa</i>			1	4	250										255
<i>Randia venezuelensis</i>				2	6										8
RUTACEAE															
<i>Zanthoxylum culantrillo</i>					107										107

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TABLE 6.—Continued.

Taxon	Flowers		Fruits				Leaves			Shoots		Roots	Resin	Unknown	Total
	Buds	Mature	Age unknown	Unripe	Ripe	Seeds	Buds	Young	Mature	Young	Flowers				
SAPINDACEAE															
<i>Allophylus cobbe</i>					4										4
<i>Paullinia cururu</i>					87										87
STERCULIACEAE															
<i>Guazuma tomentosa</i>					508										508
<i>Sterculia apetala</i>					24										24
VERBENACEAE															
<i>Vitex capitata</i>					7										7
<i>Vitex compressa</i>					20										20
<i>Vitex orinocensis</i>				5	124										129
VITACEAE															
<i>Cissus alata</i>			1		4										5
<i>Cissus sicyoides</i>					19					2					21
Unknown			1	1	6	2	1	4	1	3		13		17	49
Totals	15	19	5	311	3219	41	45	15	430	7	1	67	8	17	4200

^a Germinating seeds.^b Pith of palm fronds.

INVERTEBRATES.—Determining the identity of invertebrate material was often difficult, but of the 2,539 records that were certainly of animal origin, 56% were identified at least partially and are listed in Table 7. Each record specified the substrate or microhabitat from which the invertebrate was taken. Thus by knowing the microhabitat identity, and the identity of some of the items in these microhabitats, one can roughly guess the identity of unknown items. Appendix II lists 29 different substrates and distinguished the proportion of invertebrates identified. Below I group these substrates into broad categories and describe the typical animals found in each. The palm *Copernicia*, a rich source of invertebrate microhabitats, I subdivided into three separate categories.

Palm Crown (4.5% of feeding records): This includes the head of the trunk which is continually putting out new fronds, the bases of existing palm fronds, both green and dry, and the palm boots, the dry remains of frond bases. This substrate was a preferred foraging site, especially for females. Two species of ant, *Cephalotes* (= *Za-*

croptocerus) sp. and *Camponotus abdominalis*, were taken from the hollow palm boots. Cockroaches, tettigoniid orthopterans, and a number of different insect larval stages were commonly taken throughout the crown.

Green Palm Fronds (1.1%): As in the crown, cockroaches and grasshoppers were commonly taken, but in addition, caterpillars were an important prey item.

Dried Palm Fronds (2.1%): The most common prey items were *Cephalotes* (= *Zacroptocerus*) sp. ants that tunnel through the frond rachis. Capuchins methodically split the stem using their canines, and then mouthed, licked, and grabbed prey. Surface items were similar to those found on green fronds.

Surface of Limbs (2.6%): In the majority (78%) of these records the food items were taken slowly, as they were either relatively cryptic like the caterpillars and tree snails, or heavily armored or weaponed, like the large ants *Cephalotes atratus* and *Pachycondyla* (= *Neoponera*) sp. Items taken quickly included orthopterans, butterflies, moths, and cicadas.

TABLE 7.—Use of different animals based on frequency records.

Item	Records	Item	Records
INVERTEBRATA		COLEOPTERA	
MOLLUSCA		Grubs	41
GASTROPADA		Beetle	1
Apple snails (<i>Pomacea</i> sp.)	424	HYMENOPTERA	
Apple snails (<i>Pomacea urceus</i>)	13	Ants (<i>Cephalotes</i> sp.)	107
Land snails (unidentified)	19	Ants (<i>Camponotus abdominalis</i>)	37
ARTHROPODA		Ants (<i>Cephalotes atratus</i>)	61
ARACHNIDA		Ants (<i>Pachycondyla</i> sp.)	6
Adult spiders	12	Biting bees	10
Spider nests	11	Mud dauber wasp nest (<i>Sphecidae</i>)	1
INSECTA		Paper wasp nests (<i>Vespidae</i>)	92
Egg case (unidentified)	1	DIPLODA	
Galls	8	Millipedes	69
Larva (unidentified)	1	VERTEBRATA	
Pupa (unidentified)	15	AMPHIBIA	
Adults (unidentified)	56	Frog's eggs	15
BLATTODEA		Frogs	3
Egg cases: cockroaches	2	REPTILIA	
Cockroaches (<i>Periplaneta</i> sp.)	4	Iguanas (<i>Iguana iguana</i>)	6
MANTODEA		AVES	
Mantids	1	Egg: Chachalaca (<i>Ortalis ruficauda</i>)	12
PHASMATODEA		Egg: Ibis (<i>Mesembrinibis cayennensis</i>)	1
Stick insects	2	Egg: Tinamou (<i>Crypturellus erythropus</i>)	5
ISOPTERA		Egg: Dove (<i>Leptotila verreauxi</i>)	1
Termites	4	Egg (unidentified)	2
ORTHOPTERA		Nestling: Dove (<i>Leptotila verreauxi</i>)	2
Grasshoppers, mostly tettigonioids	108	Nestling (unidentified)	3
HEMIPTERA		Adult: Dove (<i>Columbina talpacoti</i>)	1
Cicadas	3	MAMMALIA	
Scale insects	8	Squirrel (<i>Sciurus granatensis</i>)	1
Bug	1	Not identified	1115
Larvae	2		
LEPIDOPTERA			
Caterpillars	246		
Adults	6	Total	2539

Inside Branches and Twigs (3.8%): In 35 instances, animals peeled bark off living limbs, commonly *Pithecellobium tortum*, and removed items. Most records however were of animals biting and ripping into wood to expose tunnels of *Cephalotes* (= *Zacryptocerus*) sp. ants, or to extract coleopteran grubs.

Dead Wood (1.6%): Caterpillars, coleopteran grubs, millipedes, and *Cephalotes* (= *Zacryptocerus*) sp. ants were frequently removed after animals ripped away loose bark from dead limbs and dug into rotting material.

Leaves (6.4%): Most of the items (83%) taken from this important substrate were apparently cryptic, as judged by the slow capture, and included caterpillars, pupae, arachnid nests, and snails. Scale insects were licked off leaves, and galls were mouthed off.

Dead Leaves and Leaf Debris (9.9%): This microhabitat provided the greatest wealth of food items. Ten percent of the items were taken from dried leaves still suspended in the tree, but the rest were taken while the animal sifted through leaf debris on the ground, an important

activity during the dry season. On 115 occasions, monkeys took grubs from old *Copernicia* palm seeds lying on the ground. To detect the grubs, capuchins would crack seeds between their teeth, tap the seeds together, or tap them with their fingernails. If detected, the grub was extracted after the seed had been cracked open. Snails (*Pomacea* sp.) were another item frequently discovered under the dried leaves. Snails were broken open by rapping the shells against convenient trunks. Most of the invertebrates captured by fast grabs were tettigoniid grasshoppers.

Wasp Nests: Vespid wasp nests were discovered in many locations: under palm fronds and leaves, attached to twigs and branches. Except for the younger animals, capuchins appeared to be impervious to the stings of the wasps, although I can verify their virulence. Usually the nest, once detached, was dismantled, and only the larvae eaten. The adult male often caught wasps flying around the nest.

VERTEBRATES.—Adult vertebrates were taken only irregularly. I saw an adult female capuchin eat an adult squirrel, *Sciurus granatensis*, an observation confirmed by D. Fragaszy, who worked with the same group in 1980–1981. On both occasions, squirrels were caught in trees and decapitated before being consumed. Unsuccessful attempts to extract small mammals from the crowns of palm trees were observed on a number of occasions, and once I observed capuchins attempting to liberate a *Marmosa robinsoni* murine opossum from a live trap. Catching and eating iguana lizards (*Iguana iguana*) was not uncommon (also P. August, pers. comm.). In the cases I recorded, an adult or subadult male flipped the lizard onto its back and then began eating the viscera. Muscular meat was not preferred and was often left. Frogs were taken, but in all cases discarded before they were completely consumed. Once an adult male caught a ground dove *Columbina talpacoti* in the underbrush at the forest edge.

Capuchins are probably major bird egg predators. I recorded many cases during systematic sampling. Capuchins would delicately crack the shell, break open the egg, and consume the con-

tents, often without spilling a drop. Eggs were the object of competition, so successful foragers were discreet on finding a nest and frequently moved away from the rest of the group. This would bias feeding records against these items. Most of the instances I recorded involved large, vocal birds that would defend their nests, sometimes successfully. In addition to the records in Table 7, there are records in the following years of egg predation on the following additional species: Greater Ani (*Crotophaga major*), Hoatzin (*Opisthocomus hoazin*; both S. Strahl, pers. comm.), and Gray-necked rail (*Aramides cajaneana*).

SEASONAL VARIATION.—The relative proportions of different items in the capuchin diet changed through the year (Figure 8). The decrease in the number of records in which capuchins were eating ripe fruits is accompanied by an increase in the records of their eating invertebrates ($r_s = -0.84$, $p < 0.01$). Invertebrates replaced ripe fruits as the predominant item in the diet as the number of species fruiting declines in November and December. Capuchins, especially males, were then found on the ground sifting through leaf litter and taking tettigoniid grasshoppers and *Pomacea* snails. During the dry months, the hard dry fruits of a single species, *Guazuma tomentosa*, were virtually the only fruit in the capuchin diet. Individual trees of *Ficus pertusa*, which fruits asynchronously in all months, provide some variety. *Copaifera officinalis* fruited heavily during the 1979 dry season, but not in 1978 when these records were taken. The pith of the palm frond rachis and the mature leaves of the orchid *Oncidium cebolleta* were frequently masticated.

Near the end of the dry season there were abundant unripe fruits, some of which were taken by monkeys. The first heavy rains in April or May trigger a leaf flush and an explosive rise in the phytophagous invertebrate populations. Caterpillars became an important part of the diet. The proportion of ripe fruits in the diet peaked late in August, late in the wet season, and declined at the end of the wet and beginning of the dry season. Table 8 presents the five most

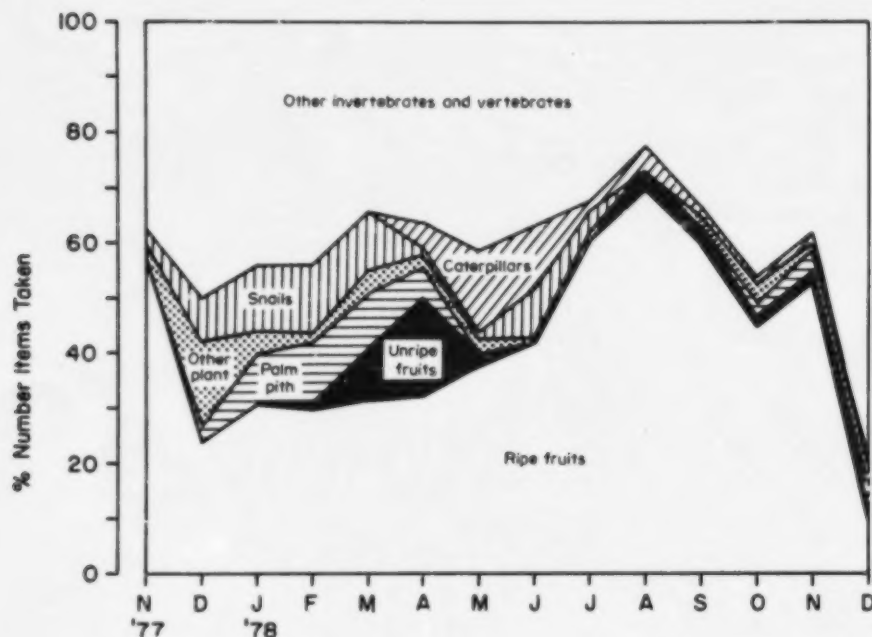


FIGURE 8.—Seasonal variation in diet as measured during the experiment.

heavily used plant items for each of the 14 months of the study. Ripe fruits predominate in the diet in every month, almost totally dominating the plant diet during the wet season.

Prediction 1: As the availability of food items drops, animals should be less selective in their choice of food items, and there should be an increase in diet diversity. This prediction derives from models of optimal diet choice (MacArthur and Pianka, 1966; Emlen, 1966; Schoener, 1971; Charnov, 1976).

Are capuchins less selective during the dry season, the time of lowest food availability? Selectivity is normally calculated as an adjusted ratio of the proportion of a food item in the diet to that of available items in the environment (Jacobs, 1974). While I do not have an independent measure of overall item availability, a decline in selectivity is indicated: At this time of year, when a species comes into fruit, it is eaten by the monkeys. During the wet season there is no such close matching between availability of a species and its use. Figures 9–11

compare monthly use of 11 important fruit species by the monkeys with their availability (if phenological information was collected). During the dry season, when no other important species was fruiting, use of *Guazuma tomentosa* fruits (Figure 10) closely tracks their availability. Even though these ripe fruits are still available in May, capuchins stop taking them as the onset of rains brings a leaf flush and the ripening of the fruits of a number of species (Figure 7). The same pattern is true for the unripe fruits and frond pith of the palm *Copernicia tectorum*, which are totally ignored once other fruits are available. During the wet season, use of a fruit matches its availability in some species such as *Genipa americana*, but not in others, such as *Randia hebecarpa*. Presumably some fruits are preferred and taken whenever they are available, while others are taken only when nothing else is available. This same pattern of selectivity can be seen when use of space is considered. Figures 9–11 also show monthly correlation coefficients (r_{xy}) between the range use of the capuchin group and the spatial distribution of each of the 11 fruit species. The

Table 8.—Rank order of five most common plant items and the percentage of the total feeding records (*N*) for each month.

Sample period	I		II		III		IV		V		<i>N</i>
	Food item	%	Food item	%	Food item	%	Food item	%	Food item	%	
1977											
Nov	<i>F. pertusa</i> ripe fruits	44	<i>R. hebecarpa</i> ripe fruits	10	<i>C. tectorum</i> leaf buds	6	<i>M. trilobata</i> ripe fruits	2	<i>M. undulata</i> unripe fruits	0.4	256
Dec	<i>O. cebolleta</i> mature leaves	8	<i>M. trilobata</i> ripe fruits	8	<i>R. hebecarpa</i> ripe fruits	7	<i>G. tomentosa</i> ripe fruits	4	<i>C. tectorum</i> frond rachis	3	285
1978											
Jan	<i>G. tomentosa</i> ripe fruits	30	<i>C. tectorum</i> frond rachis	9	<i>O. cebolleta</i> mature leaves	2	<i>C. vitifolium</i> roots	2	<i>R. hebecarpa</i> ripe fruits	0.6	513
Feb	<i>G. tomentosa</i> ripe fruits	25	<i>C. tectorum</i> frond rachis	11	<i>F. pertusa</i> ripe fruits	4	<i>C. officinalis</i> ripe fruits	1	<i>O. cebolleta</i> flowers	0.6	670
Mar	<i>G. tomentosa</i> ripe fruits	17	<i>C. tectorum</i> frond rachis	10	<i>C. tectorum</i> unripe fruits	8	<i>F. pertusa</i> ripe fruits	6	<i>F. trigonata</i> ripe fruits	3	848
Apr	<i>C. tectorum</i> unripe fruits	15	<i>C. collococca</i> ripe fruits	14	<i>G. americana</i> ripe fruits	6	<i>C. tectorum</i> frond rachis	6	<i>G. tomentosa</i> ripe fruits	4	717
May	<i>G. americana</i> ripe fruits	26	<i>C. collococca</i> ripe fruits	9	<i>C. coccolobifolia</i> ripe fruits	2	<i>V. orinocensis</i> unripe fruits	1	<i>H. polyhrizus</i> flowers	0.7	609
Jun	<i>V. orinocensis</i> ripe fruits	22	<i>G. americana</i> ripe fruits	9	<i>F. pertusa</i> ripe fruits	7	<i>C. collococca</i> ripe fruits	2	<i>V. capitata</i> ripe fruits	1	507
Jul	<i>F. pertusa</i> ripe fruits	43	<i>Z. culantrillo</i> ripe fruits	8	<i>P. serrulata</i> ripe fruits	3	<i>V. orinocensis</i> ripe fruits	2	<i>F. trigonata</i> ripe fruits	1	591
Aug	<i>A. jahnii</i> ripe fruits	25	<i>F. pertusa</i> ripe fruits	21	<i>Z. culantrillo</i> ripe fruits	12	<i>P. cururu</i> ripe fruits	3	<i>V. compressa</i> ripe fruits	3	517
Sep	<i>F. trigonata</i> ripe fruits	17	<i>P. cururu</i> ripe fruits	13	<i>F. pertusa</i> ripe fruits	12	<i>G. divaricata</i> ripe fruits	8	<i>P. anceps</i> ripe fruits	4	533
Oct	<i>F. trigonata</i> ripe fruits	20	<i>F. pertusa</i> ripe fruits	8	<i>P. anceps</i> ripe fruits	7	<i>D. ierensis</i> ripe fruits	3	<i>R. hebecarpa</i> ripe fruits	3	588
Nov	<i>R. hebecarpa</i> ripe fruits	30	<i>F. pertusa</i> ripe fruits	14	<i>D. ierensis</i> ripe fruits	6	<i>C. tectorum</i> leaf buds	2	<i>S. setuloso-ciliata</i> seeds	2	607
Dec	<i>S. apetala</i> ripe fruits	6	<i>C. tectorum</i> frond rachis	4	<i>C. tectorum</i> leaf buds	3	<i>F. trigonata</i> ripe fruits	2	<i>C. vitifolium</i> roots	2	417

higher the correlation coefficient, the more closely did the animals match their use of space to that of the fruit species. Matching is tight in the dry season (see *Guazuma*) but not always in the wet (see *Cordia*). The increase in selectivity with overall resource abundance indicates that animals can retain information on what species are in fruit.

This increase in selectivity, however, is not associated with a decrease in diet diversity. Table 9

gives the diversity of use of all plant items for each month of the study. Diversity is high during the transition period between the dry and wet seasons (March and April), between the wet and dry (September and October), and during December when very few species are in fruit. In these months a number of different items are available but none are very abundant. The expected negative correlation between diet diversity and selectivity is not

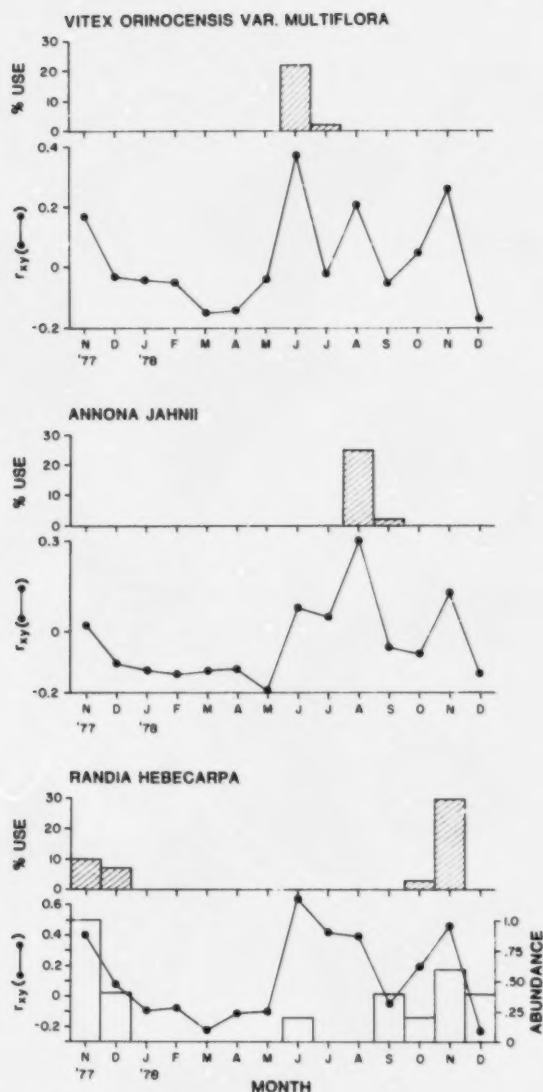


FIGURE 9.—Use (percentage of the total feeding records) of ripe fruits of *Vitex orinocensis*, *Annona jahnii*, and *Randia hebecarpa* (shaded bar graphs). All three species occur predominantly on sandy medano ridges. Correlation between the spatial distribution of each species and the group's use of space in each month (r_{xy}) (lower line). For *Randia*, relative availability of ripe fruits based on phenology data (open bar graphs).

FIGURE 10 (Top).—Use (percentage of total feeding records) of ripe fruits of *Guazuma tomentosa*, *Genipa americana*, and *Cordia alliodora*, and use of unripe fruit and vegetal matter of palm *Copernicia tectorum* (upper bar graphs). Correlation between the spatial distribution of each species and the group's use of space in each month (r_{xy}) (lower line). Relative availability of ripe fruits of *Guazuma*, *Genipa*, and *Cordia* and of unripe fruits, frond buds, and young fronds of *Copernicia* based on phenology data (lower bar graphs).

FIGURE 11 (Bottom).—Use (percentage of total feeding records) of ripe fruits of *Zanthoxylum culantrillo*, *Guettarda divaricata*, *Ficus trigonata*, and *Ficus pertusa* (upper bar graphs). Correlation between the spatial distribution of each species and the group's use of space in each month (r_{xy}) (lower line). Relative availability of ripe fruits of the *Ficus* species based on phenology data (lower bar graphs).

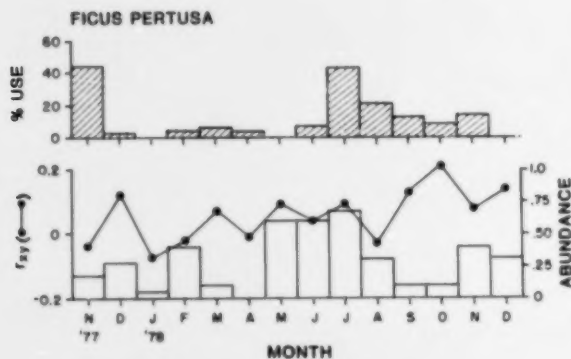
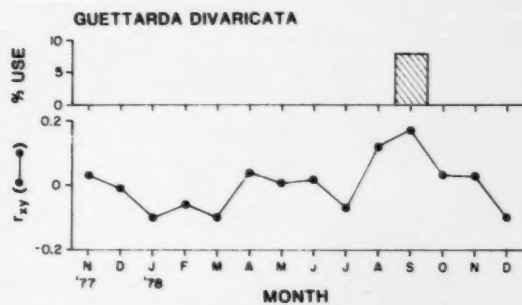
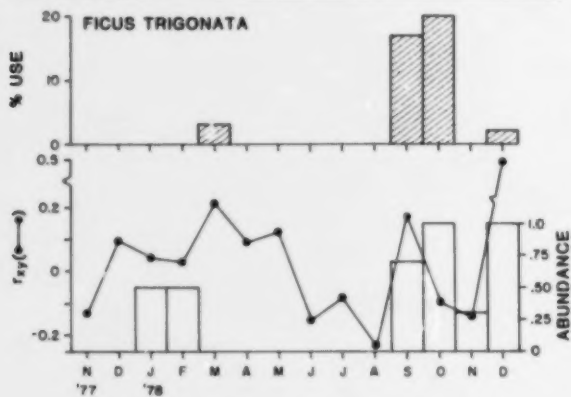
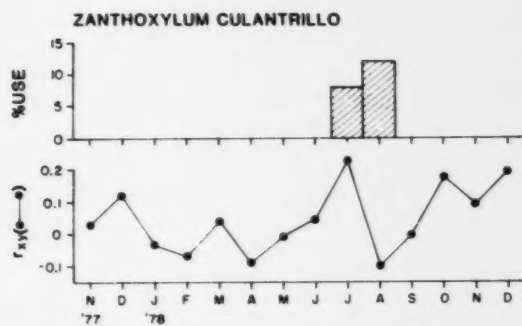
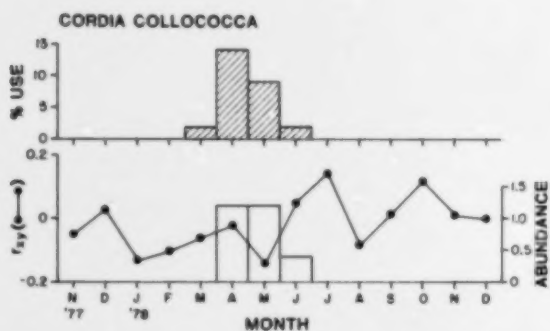
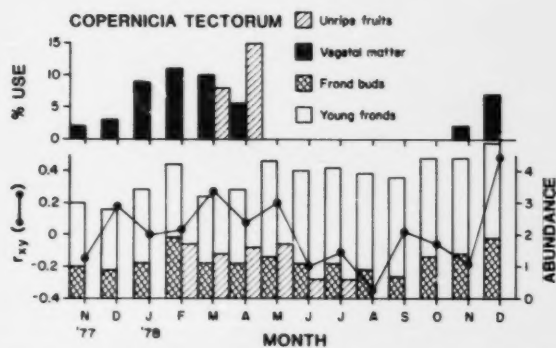
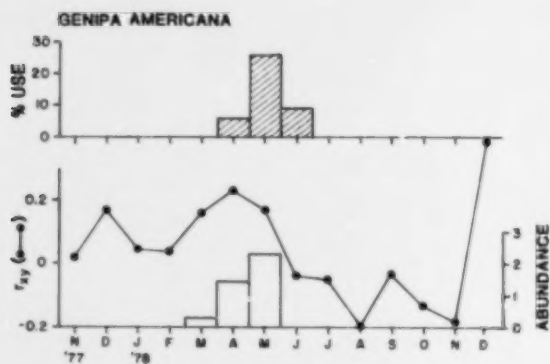
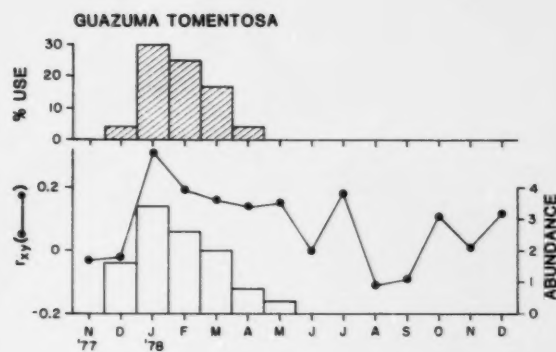
TABLE 9.—Diversity of use of plant items using the Shannon-Wiener index ($H' = -\sum (p_i \ln p_i)$), where p_i is the proportion of frequency records falling into the i^{th} category of items.

Month	H'	Month	H'
1977		May	1.510
Nov	1.015	Jun	1.335
Dec	2.328	Jul	1.223
1978		Aug	1.927
Jan	1.219	Sep	2.216
Feb	1.577	Oct	2.189
Mar	2.226	Nov	1.683
Apr	2.111	Dec	2.347

realized because the diversity of items actually available in a given month varies.

TIME BUDGETS

Capuchins spend almost 70% of their active hours, averaging across months, searching for and processing food. In 22.4% of the 15,596 activity records, the subject animal was taking or attempting to take animal material, in 17% it was taking plant material, and in 1.4% it was drinking. In 22.2% of records the subject was moving, and in 5.8% it was scanning, activities associated



with foraging for invertebrates and moving between fruit trees. Thus capuchins devote more time to invertebrate foraging than to feeding on plant material, though most of the items ingested are of plant origin, and certainly the latter form the bulk of the diet.

Different age-sex classes partition their time differently (Figure 12). Males rest a higher proportion of time when compared to equal-age female classes, while female classes engage in social interactions more often. Moving is the predominant infant activity, for these animals must move almost continually to keep up with the rest of the group. With the exception of infants, who feed and forage infrequently, individuals spend between 45% and 55% of their time actively foraging and feeding, and almost 20% of their time moving. The proportion of time feeding on plant material is similar among classes. Males spend more time searching for and processing food items while females take invertebrates more. This results from females consistently having more success feeding on invertebrates, while males spend more time looking for, and attempting to capture relatively rare but "high quality" items. For instance, males accounted for over 90% of the vertebrate captures.

SEASONAL VARIATION.—The amount of time allocated to foraging varies considerably through the year (Figure 13). In April 1978, at the end of the dry season, for instance, animals spent 58% of their time foraging and 19% moving. A month later, after the onset of the rains, they spent 43% of their time foraging and 17% moving. During the dry season there is little time available for non-foraging activities. Social interactions, from time budget highs of 20% at the start of the wet season, fall to 6% at the end of the dry season. Some behaviors, such as play (2.5% of the yearly time budget) disappear entirely during the dry season (also see Muller-Schwarze et al., 1982). The following predictions address the general question: what determines the proportion of time allocated to foraging?

Prediction 2a: Animals should allocate more time to foraging when resources are scarce.

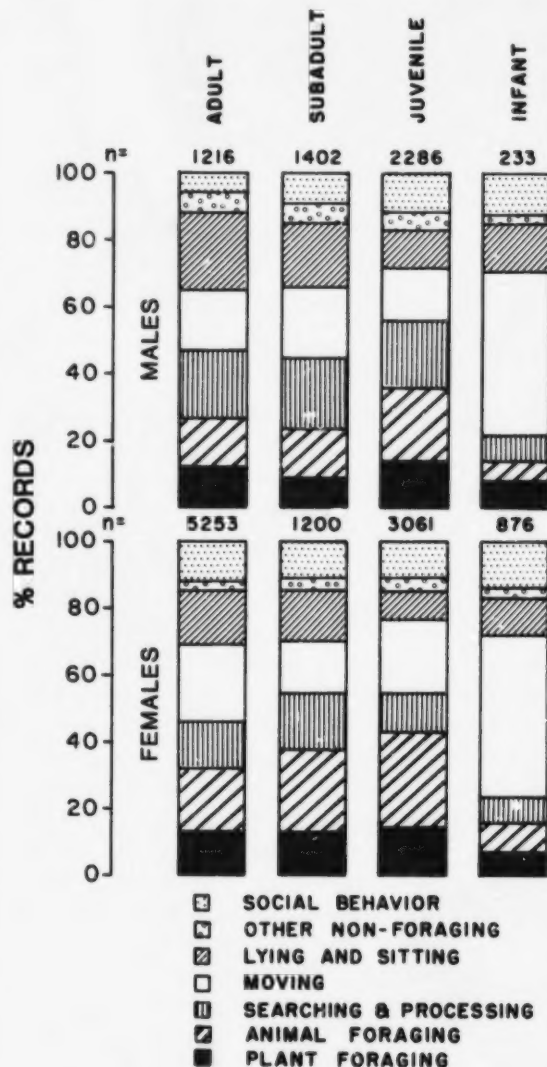


FIGURE 12.—Time budgets of different age-sex classes (n = number of observations in each class).

This assumes that animals forage until they meet their daily energy requirements.

As I have no index of overall resource abundance, this could not be tested directly. However, in the wet season many species of trees fruit and flush their leaves, and phytophagous insects track plant productivity. As expected, time allocated

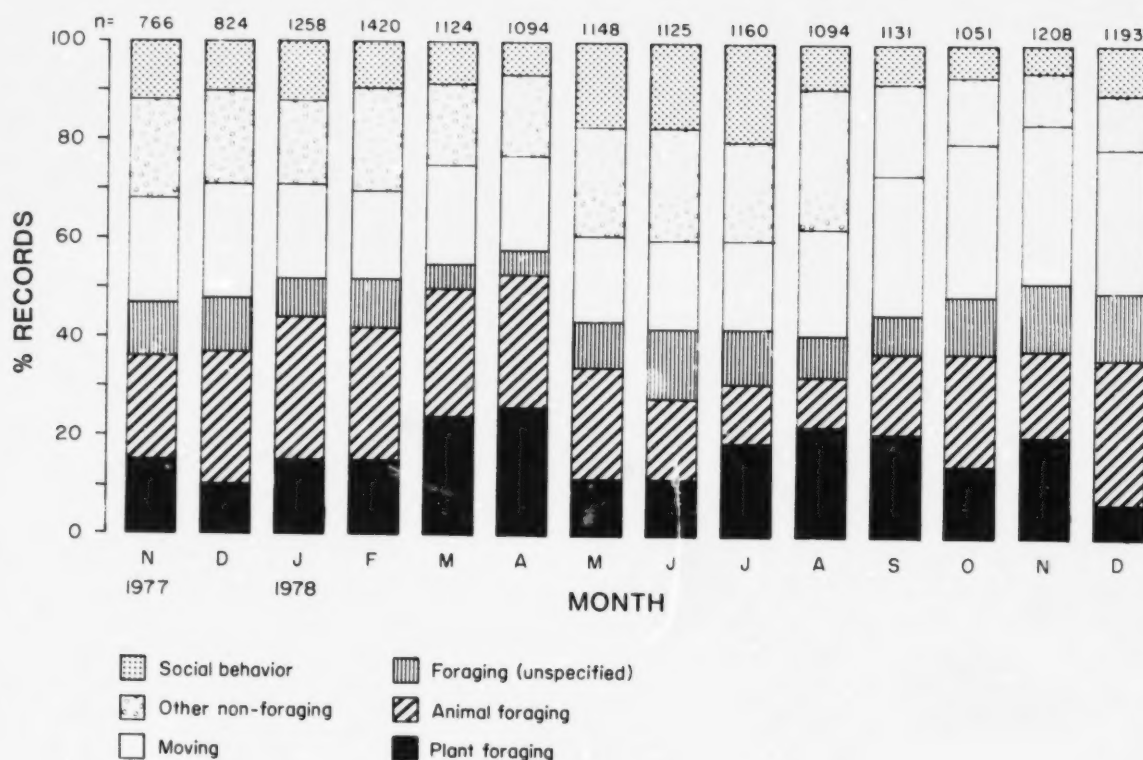


FIGURE 13.—Annual variation in the time budgets of group members (n = number of observations in each month).

to foraging was negatively correlated with monthly rainfall ($r = -0.82$, $p < 0.01$).

Prediction 2b: An alternate prediction is that animals should allocate more time to foraging in months when they rely on invertebrates, and less time when they rely on ripe fruit. This prediction assumes that the time allocated to foraging might depend on the seasonal availability of specific food items and their handling times. During wet months, capuchins allocate more time to feeding on fruit ($r = 0.82$, $p < 0.01$), while in dry months they forage for invertebrates ($r = 0.85$, $p < 0.01$).

Foraging for invertebrates is time-consuming, both because invertebrates are scattered throughout the habitat, and because they are either cryptic, and therefore difficult to find, or mobile, and therefore difficult to catch. In con-

trast, the local concentration of fruit allows animals to quickly ingest much more fruit than they can digest at one time.

In months when animals forage heavily for invertebrates, they tend to allocate more time to foraging ($r = 0.26$, $p < 0.05$), but the correlation is not significant, presumably because harvest rates of invertebrates vary across months. Harvest rates of caterpillars, for instance, are extremely high at the beginning of the wet season. As predicted, in months when animals are feeding on ripe fruits, they spend less time foraging ($r = -0.67$, $p < 0.01$).

These results do not conclusively reject or support either prediction 2a or 2b. An alternative approach is to examine if different age-sex classes allocate foraging time differently with season. Predictions 3a through 3d follow this approach.

TABLE 10.—Variation among age-sex classes across months in % of time foraging. Mean was calculated using the arcsin transformation. Rainfall data were collected at the Hato Masaguaral ranch house, approximately 4 km from the study site.

Month	Rainfall (mm)	Adult		Subadult		Juvenile		Mean
		Male	Female	Male	Female	Male	Female	
1977								
Nov	126.0	35.5	41.0	44.8	54.7	49.5	62.0	47.9
Dec	0.0	49.4	45.1	49.0	45.5	55.2	52.0	49.3
1978								
Jan	0.0	48.0	53.7	54.5	51.0	62.9	52.9	53.8
Feb	0.0	54.7	52.7	51.2	50.8	56.9	61.7	54.7
Mar	2.1	54.5	56.5	41.4	56.7	61.4	63.1	55.6
Apr	70.9	53.2	51.4	49.5	67.8	63.2	69.4	59.2
May	179.6	27.9	43.7	33.0	43.0	51.6	56.0	42.4
Jun	328.0	35.4	37.0	38.0	56.8	52.5	43.8	43.9
Jul	180.4	37.0	37.5	37.0	50.7	50.6	47.9	42.5
Aug	396.5	49.3	34.4	32.4	53.6	51.4	47.9	44.8
Sep	179.0	41.1	42.1	34.0	63.2	51.3	53.5	47.6
Oct	145.1	47.4	52.8	46.2	58.5	48.6	53.7	51.2
Nov	49.8	52.6	51.7	56.5	70.2	60.2	54.5	57.7
Dec	20.4	61.8	49.9	64.9	48.1	62.2	57.3	57.5
Mean		46.2	46.3	42.5	55.1	55.6	55.4	

TABLE 11.—Variation among age-sex classes across seasons in % of time foraging. Dry season defined in this analysis as months with less than 100 mm rainfall.

Season	Adult		Subadult		Juvenile		Mean
	Male	Female	Male	Female	Male	Female	
Dry	53.5	51.6	52.4	55.9	60.3	58.8	55.4
Wet	39.0	41.2	37.9	54.4	50.8	52.1	45.8

Prediction 3a: All age-sex classes allocate more time to foraging when resources are scarce. As energy requirements scale approximately to body size (McNab, 1983), larger age-sex classes should consistently allocate more time to foraging.

Variation in foraging time among age-sex classes and across seasons was tested using a two-way ANOVA on transformed proportions of foraging time. The arcsin transformation of proportions meets the assumptions of the analysis of variance (Sokal and Rohlf, 1969). For the age-

sex classes I considered only adults, subadults, and juveniles of the two sexes. I defined dry months as those with a total precipitation of less than 100 mm, and wet as those with more than 100 mm (see Walter, 1971). The proportion of time spent foraging was the dependent variable. There was a significant effect of season on the amount of foraging ($F = 51.6$, $df = 1, 72$, $p < 0.01$): animals of all classes foraged more during the dry season (Table 10). Differences among age-sex classes (Table 11) were also significant ($F = 10.3$, $df = 5, 72$, $p < 0.05$), but it was the larger age-sex classes (adult males, females and subadult males) that foraged less than the other classes.

TABLE 12.—Variation in foraging activity among age-sex classes; percentage of foraging time allocated to each class of items or foraging microhabitat (n = number of observed activities; in parentheses for each class).

Foraging activity	Adult		Subadult		Juvenile		Immature	
	Male (576)	Female (2447)	Male (651)	Female (660)	Male (1290)	Female (1706)	Male (52)	Female (211)
Plant material								
Ripe fruits	31.4	26.3	23.8	20.8	26.4	24.9	46.2	37.4
Unripe fruits	1.4	2.0	1.0	2.9	1.9	2.1	1.9	3.3
Roots	2.1	0.0	1.7	0.2	0.7	0.0	0.0	0.0
Palm pith	0.1	4.2	1.1	4.2	3.1	3.7	3.8	2.4
Animal material								
Snails (<i>Pomacea</i>)	5.2	1.4	2.9	3.3	6.0	1.6	0.0	0.1
Wasp nests	1.7	0.6	0.8	0.6	0.3	0.2	0.0	0.0
Leaf litter	3.8	1.5	4.2	2.6	4.2	2.0	0.0	0.3
On surfaces	15.6	7.8	14.3	4.1	13.8	7.9	0.0	0.2
Inside branches, twigs, etc.	6.0	8.3	8.9	10.8	8.8	10.7	11.5	5.2
In palm crowns	0.0	21.1	0.1	17.7	4.1	25.4	9.6	19.0
Scanning	19.8	12.8	24.3	12.9	11.4	6.0	0.0	0.0
Other	12.9	14.0	16.9	19.9	19.3	15.5	27.0	31.9

In addition, though adult and subadult males are considerably larger than adult females, the time they spent foraging was similar. They allocated slightly more time to foraging in the dry season, and slightly less in the wet season. This difference in the response of the two sexes to the different seasons just reaches significance (ANOVA interaction $F = 2.4$, $df = 5,72$, $p < 0.05$). The proportional increase in foraging time from wet to dry season was higher in the adult and subadult males (14.5% and 14.5%) than the equivalent female age classes (10.4% and 1.5%). For juveniles the sex difference in the increase in foraging time was less pronounced (9.5% for males, 6.7% for females). These results suggest that neither overall resource abundance nor body size determines the foraging time required to meet daily energy needs.

Prediction 3b: If the time allocated to foraging depends on the specific food items taken, then differences in foraging time among age-sex classes should reflect differences in their choice of food items and foraging microhabitats. The processing time of different food

items varies, and different microhabitats have different food yields.

Different age-sex classes forage on different food items and in different microhabitats (Table 12; Robinson, 1981; Fragaszy, in press). Except for infants, males of all age classes spend more time on the ground than females of the equivalent class (Robinson, 1981). As a result, the time they forage through ground leaf litter is higher, and they feed more on apple snails (*Pomacea* sp.), tettigoniid grasshoppers, and plant roots. Females spend more time foraging off the ground, and sift especially through debris in palm crowns, and between palm boots. Despite their smaller canines (Orlosky, 1981), they allocate more time to splitting twigs and biting into branches to extract grubs, ants and millipedes. Males take invertebrates more from surfaces.

These differences in diet and choice of foraging microhabitat are probably largely responsible for the differences in foraging time between adult and juvenile age classes. Juveniles probably must also allocate more time to foraging because they are less skilled at catching and finding food items, and know less about the location of food.

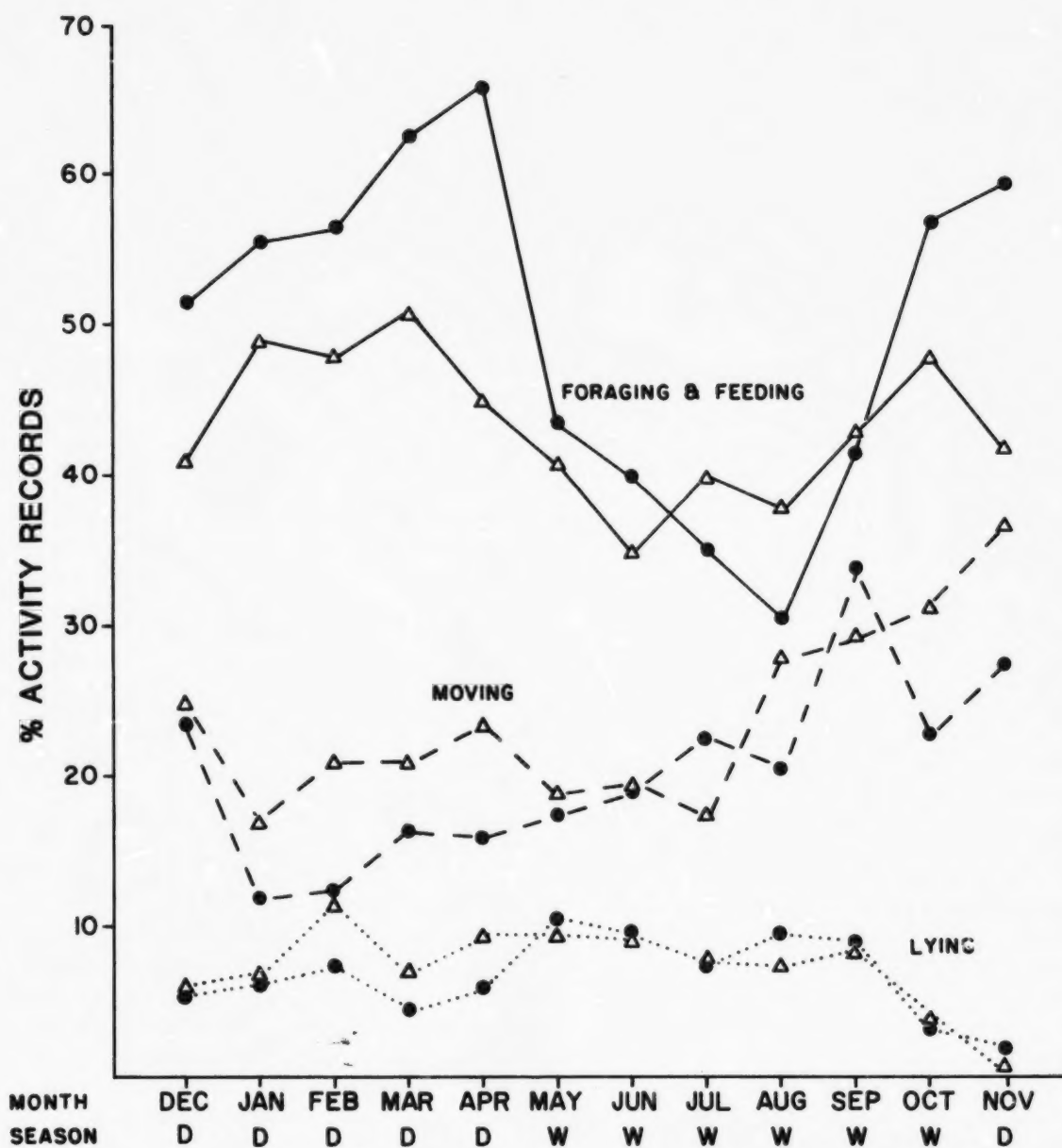


FIGURE 14.—Percentage of time allocated to feeding and foraging, moving, and lying down, by pregnant and lactating females (closed circles), and by other females (open triangles).

Fragaszy (in press) reports that juveniles are less efficient foragers, where efficiency is defined as the proportion of foraging samples in which an-

imals successfully ingested an item. While adult and subadult males forage in different microhabitats and have different diets than females, these

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factors do not account for the variation in allocation of foraging time.

Prediction 3c: Adult females should forage more than expected on the basis of body size because of the energetic costs they incur during gestation and especially lactation. Females give birth at the beginning of the rains; therefore the higher energy costs of lactation (versus gestation; Miguela, 1969; Studier et al., 1973) occurs during the wet season. Thus females as a group would not show the same decrease in foraging time during the wet season as males.

To test this prediction I compared the time allocated to foraging by pregnant and non-pregnant females in the dry season of 1978, and by lactating and non-lactating females during the wet season. Of the seven adult females in the group in 1978, three were pregnant. One infant was born in late May and two more in early June. All survived their first year. As expected (Figure 14), the three pregnant females foraged significantly more than the four non-reproducing females during the six months of the dry season while they were pregnant ($t = 3.13$, $df = 10$, $p < 0.01$, one-tailed test, all proportions transformed). They also moved significantly less ($t = 2.32$, $df = 10$, $p < 0.05$, two-tailed test), but differences in the proportion of time resting and lying were not significant. This time of year is especially severe on pregnant females: at the height of the dry season and during the last months of their pregnancy, females spend over 90% of their daytime foraging and moving. Contrary to prediction however, lactating females did not forage more in the six months of wet season ($t = 0.54$, $df = 10$, $p > 0.05$).

Neither body size nor reproductive condition, therefore, accounts for the observed variation in foraging time shown by different age-sex classes in different seasons. This suggests that the factors that determine or limit foraging time of the different age-sex classes vary with the season.

Prediction 3d: During the dry season when resources are limited, foraging time should be proportional to the daily energy requirements

of the animals. During the wet season when resources are abundant, foraging time should be determined by the digestive capacities of the animals. These capacities, in animals with the same digestive systems and the same diet, do not vary appreciably with body size (Janis, 1976; Clutton-Brock and Harvey, 1983). Animals should ingest much more than their daily energy requirements and store the excess, presumably as fat.

During the dry season, as I have already shown, pregnant females foraged more than non-pregnant. As predicted, the larger males also foraged more than these females ($t = 3.2$, $df = 12$, $p < 0.01$). During the wet season, there was no difference in foraging time between lactating and non-lactating females, and as predicted, males did not forage more than lactating ($t = 0.12$, $df = 10$, $p > 0.05$) nor non-lactating females ($t = 0.53$, $df = 12$, $p > 0.05$).

In summary, the time allocated to foraging varies with season. Both overall resource abundance and the availability of specific food items (e.g., ripe fruit versus invertebrates) potentially determine the foraging time required to meet daily energy requirements. Daily energy requirements, however, only determine foraging time in the dry season. In the wet season, foraging time is determined by the digestive capacities of animals.

MOVEMENTS

Figure 15 illustrates a superposition of all movements of the group's center of mass for the 99 days that the group's movements were traced. Sleeping trees were not randomly distributed across the range, although they were common enough not to affect significantly the direction of movement. For sleeping, capuchins preferred certain clumps of large spreading trees, such as *Pterocarpus acapulcensis* and *Copaifera officinalis* at the forest edge. Areas most heavily used for travel were routes between areas where animals foraged and those sites used for sleeping. The converging lines of group movement in the northeast represent a favored drinking site on

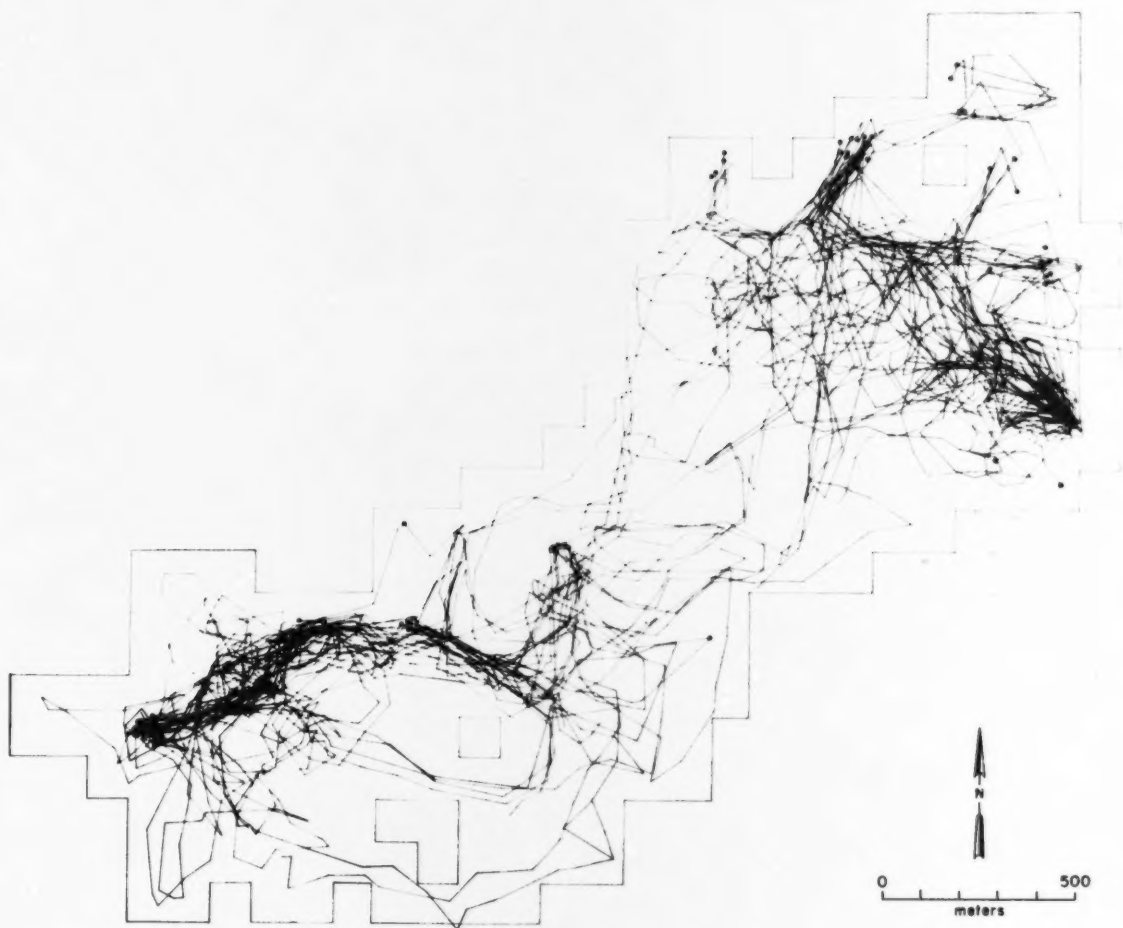


FIGURE 15.—Superposition of the movements of the group's center of mass from all the days in which such information was taken. Closed circles represent sleeping areas.

the Caño Caracol to which the group moved up to four times daily during the dry season.

Based on the 72 days in which I followed the group from its exit from the sleeping grove in the morning until it entered a grove in the evening, the mean daily path length was 2141 m, with a range of 1046–3580 m (Table 13 and Figure 16). Figure 17 presents the distribution of distances moved in the half-hour periods (step lengths). The modal category of distance moved in a half hour was 60–79 m, and the mean distance was 91.0 m. If the speed of group move-

ment is random, the distribution should follow a two dimensional Maxwell-Boltzmann distribution (Waser, 1976, 1982; De Vita et al., 1982), and the group would be as likely to spend time in any area. The fit to the expected distribution deviates from expectation (Figure 17), however, in that there are more short and more long movements than expected ($\chi^2 = 6724.9$, $p < 0.001$). This is consistent with the expectation that animals respond to resource availabilities, and move more rapidly through areas of low abundance, more slowly through areas of high

TABLE 13.—Distance travelled and half-hour step length statistics.

Month	Average daily path length (m)	Coefficient of variation		H'_s (step lengths)	n step lengths	
		Ranked	(%)		Ranked	
1977						
Nov	1598	14	36	2.134	14	120
Dec	1868	12	20	2.260	9	111
1978						
Jan	1690	13	13	2.214	11	121
Feb	1895	10	15	2.251	10	124
Mar	2165	7	22	2.417	4	124
Apr	2350	6	21	2.406	5	126
May	2046	9	8	2.271	8	120
Jun	2095	8	29	2.325	7	123
Jul	1878	11	19	2.150	13	123
Aug	2430	3	27	2.492	1	124
Sep	2426	4	16	2.472	2	121
Oct	2563	2	15	2.433	3	123
Nov	2716	1	12	2.369	6	130
Dec	2397	5	8	2.197	12	123

To provide an index of heterogeneity of step lengths within months, I used the Shannon-Wiener index of diversity,

$$H' = -\sum_{i=1}^n (p_i \ln p_i).$$

This index is appropriate in this analysis because it is not affected by differences among months in average daily path length, and it is relatively insensitive to extremely long steps that often had nothing to do with foraging (e.g., rapid movements to sleeping and drinking sites). It is sensitive to the number of steps, but in this comparison, these were equal or nearly so across months. Table 13 presents H'_s values for all 14 months.

Turning angles were not randomly distributed. The preferred or mean direction (Batschelet, 1965, 1972) was calculated (Table 14), and indicated that in all months daily movement tended to be forward. Minus signs indicate a mean direction to the right of straight ahead, and plus signs a mean direction to the left. The modified Rayleigh test (Batschelet, 1972) calculates the significance of the deviation of the ob-

served distribution from uniformity. In all months there was a highly significant deviation from uniformity. Finally I examined the symmetry of movement (see Batschelet, 1965): did the group deviate significantly from straight ahead, either to the left or to the right? In only two of the 14 months were mean angles significantly different from 0° , and in both they only just reached the 0.05 significance level. In all months and over the whole year, the group showed a strong tendency to move forward, rather than to backtrack, and exhibited little if any directional asymmetry either to the left or right. Figure 18 illustrates the distribution of angles between half-hour steps. Most angles were in the first and fourth quadrants: Not only is the mean direction forward but most movements are forward. I calculated two more indices of angular movement. Average turning angle is the mean angle (Batschelet, 1972) of turn, either to the left or right. With higher average angles, the group will have more of a tendency to backtrack. Average turning angles across months (Table 14) are inversely correlated with average daily path

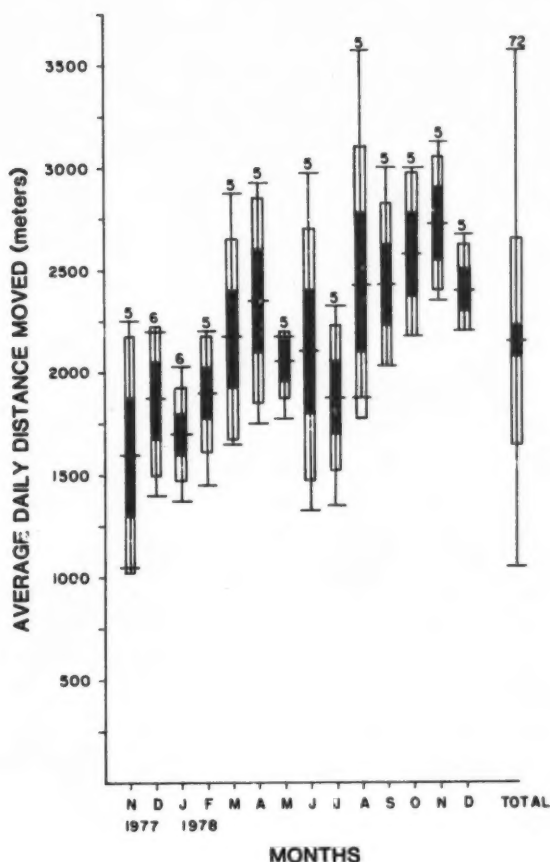


FIGURE 16.—Average daily path length during the 14 study months. For each month the graph gives the mean (center horizontal line), the standard error of the mean (black bar), the standard deviation (clear bar), and the range (vertical line). Numbers above each bar are the number of sample days in each month.

length ($r_s = -0.66$, $p < 0.01$), which indicates that long daily movements are associated with a forward movement rather than a tendency to backtrack. The second index, the diversity of turning angles H'_m within months, was a measure of the tortuosity of the daily path in a given month. Smooth paths, be they linear or curved, should have a low turning angle diversity.

SEASONAL VARIATION.—There is considerable monthly variation in the average daily distance travelled, and in the heterogeneity of half-hour

steps and turning angles (Tables 13 and 14, Figure 16). If this variation is a consequence of different distributions of resources, how do animals adjust their movements to take advantage of resource availabilities?

Some models of animal movement assume that animals have no information on the specific location of resources and so must search for them. A first set of predictions (4a, 4b) assume that animals have information on resource availability derived from their recent rate of encounter with food, and that in response to this information they allocate time to foraging and move accordingly. Movements should be predictable either from the overall foraging time of animals (prediction 4a) or the time foraging for different food items (prediction 4b).

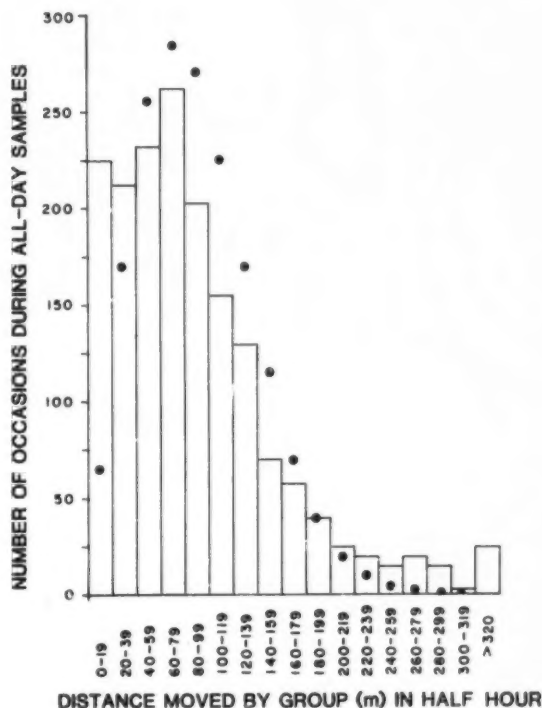


FIGURE 17.—Distribution of distances moved in all half-hour periods ($\approx$ step lengths). Closed circles are the values expected from a random distribution of half-hour movements (two-dimensional Maxwell-Boltzmann).

TABLE 14.—Turning angle statistics.

Month	Directionality or mean direction	Modified Rayleigh u	Signifi- cance	Signifi- cance of deviation from 0°	Average turning angle	Ranked	H'_m turning angle	Ranked	n turning angles
1977									
Nov	-0.44°	5.50	0.0001	ns	54.62°	2	2.675	2	91
Dec	-2.08°	9.33	0.0001	ns	37.37°	12	2.262	14	95
1978									
Jan	12.93°	6.40	0.0001	ns	51.17°	5	2.563	5	101
Feb	18.41°	5.18	0.0001	0.05	55.32°	1	2.675	1	95
Mar	3.37°	7.46	0.0001	ns	45.86°	7	2.478	9	104
Apr	-10.86°	8.24	0.0001	ns	45.81°	8	2.556	7	110
May	-3.31°	7.62	0.0001	ns	48.51°	6	2.526	8	109
Jun	-13.21°	6.38	0.0001	ns	53.78°	3	2.628	3	109
Jul	9.64°	6.64	0.0001	ns	51.66°	4	2.579	4	103
Aug	-4.81°	7.81	0.0001	ns	45.42°	9	2.563	6	107
Sep	2.82°	8.38	0.0001	ns	41.41°	10	2.467	10	108
Oct	-2.47°	9.31	0.0001	ns	32.00°	14	2.419	11	115
Nov	-1.10°	10.20	0.0001	ns	37.39°	11	2.292	13	119
Dec	-8.61°	10.68	0.0001	0.05	33.02°	13	2.306	12	118
Total	-0.99	29.21	0.0001	ns					1484

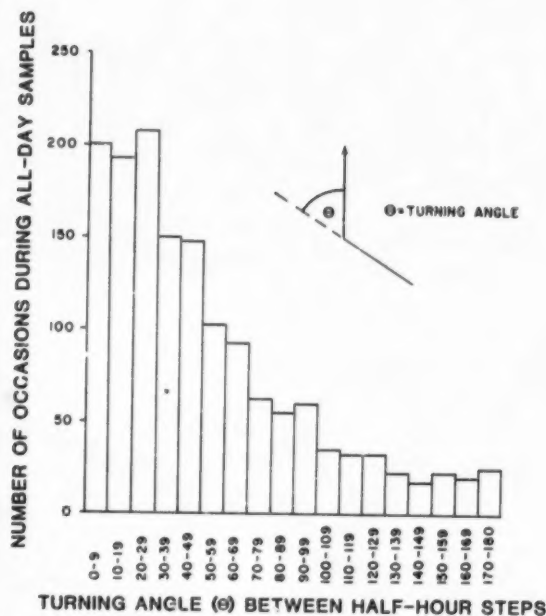


FIGURE 18.—Distribution of turning angles between all half-hour steps.

Prediction 4a: Movements should depend on time spent foraging (see Clutton-Brock, 1977; Raemaekers, 1980), which in turn should depend on the encounter rate with food. Capuchins should travel further each day when resources are scarce. As capuchins forage less when they spend more time eating fruits, daily path length should be low in months when animals rely on fruits.

To test this prediction I ranked the average daily path length for each month and compared these to the ranked proportions of time allocated to foraging, fruit eating, etc. Average path length was not related to the time spent foraging ($r_s = -0.09$, $p > 0.05$), nor to feeding time on fruit ($r_s = 0.35$, $p > 0.05$). Daily path length is also positively correlated, though not significantly, with monthly precipitation ($r_s = 0.38$, $p > 0.05$). Contrary to prediction, daily path length is *higher* when resources are abundant.

Prediction 4b: Alternatively, movements

should depend on the time allocated to foraging for specific food items. This would follow if movements depended not on overall resource availability, but on the different spatial distributions of the specific foods used each month. Three specific tests follow. (1) When capuchins forage for foods that occur in only a few locations, daily path length should be high. This is expected because much of the daily range would cross areas relatively poor in resources, and finding resources that are unevenly distributed in space would be more difficult than encountering uniform resources. It is also likely that food patches would often be distant from areas associated with other activities, such as drinking and sleeping sites, and this would lengthen daily path length. (2) If the group is able to adjust its speed to local resource abundances, the movements should be more heterogeneous in months when resources are heterogeneously distributed. (3) The daily number of half-hour periods during which the group did not move at all should be high when groups are exploiting spatially uneven resources.

The results are equivocal. (1) Foods of plant origin, especially ripe fruits, are less homogeneously distributed than invertebrates. Contrary to prediction, however, daily path length did not correlate significantly with the ratio of time spent foraging on plant versus animal material ($r_s = 0.38$, $p > 0.05$), nor with the time feeding on fruit. (2) Step length diversity (H'_s) did correlate with the plant : animal foraging ratio ($r_s = 0.46$, $p < 0.05$), but not with the proportion of ripe fruit-foraging records ($r_s = 0.31$, $p > 0.05$). (3) The number of half-hour periods in which the group was stationary did not correlate either with the percentage of foraging time taking fruit ($r_s = -0.07$, $p > 0.05$) or with the ratio of time spent feeding on plant versus animal matter ($r_s = 0.02$, $p > 0.05$).

These results indicate that neither the overall allocation of foraging time nor the amount of time capuchins spent foraging on specific items is a good predictor of group movements. A sec-

ond set of predictions (5a, 5b) derives from models that assume that animals, in addition to having information on resource abundances, also have some information on the typical spatial distributions of specific resources; and move in paths that maximize encounter rate with food (Smith, 1974a, 1974b; Thomas, 1974; Hassell, 1978; Zach and Falls, 1977).

Prediction 5a: "Area restricted searches" should occur in months when resources are patchily distributed in space. These searches are characterized by tortuous movements, a consequence of increases in turning angles following the discovery of a food item.

As an index of the food patchiness in each month, I used the Morisita's index value of the fruit tree most important at that time. This measures the extent to which trees of a species are patchily distributed in space. One exception was the fig *Ficus pertusa*, which I considered to be the most patchily distributed resource, because although trees fruit throughout the year, few do so at any given time. Those that do so are often close together. As a measure of the tortuosity of the movement path of the capuchin group, I used the average turning angle and the diversity of turning angles H'_a . Contrary to expectation, the correlation between species patchiness and both average turning angle ($r_s = -0.27$) and diversity of turning angles ($r_s = -0.19$) were not significant, and any tendencies were opposite to the direction predicted.

Prediction 5b: The tendency of the capuchin group to turn back rather than to move forward should be greater in months when plant material, and ripe fruits in particular, are important in the diet. Whether a group will return to an area should depend on the extent to which the resource was depleted during the first visit, and the resource's capacity for renewal (Charnov et al., 1976; Waser and Wiley, 1979; Waser, 1981). When resources are renewed rapidly, or not depleted quickly, there is no turning around disadvantage (Waser and Wiley, 1979). If there is, in addition, an advan-

tage to turning around, animals should tend to double back rather than to move on. Microhabitats containing invertebrates are not rapidly depleted, for many invertebrates can retire into refugia, and they are renewable, for the area can be rapidly recolonized from adjacent areas. Invertebrate distribution in space is relatively homogeneous, however, so there is little advantage to turning around. With fruit trees, on the other hand, there is an advantage in returning to a tree that has already been located, if the source has not already been depleted or if additional fruit has ripened. Most of the tree species that are important to capuchins produce large fruit crops that are not easily depleted, even by a large capuchin group. Some, such as the *Ficus* species, produce crops over an extended period of time (August, 1981).

Tendency to backtrack was measured by calculating the average turning angle between steps, and counting the number of times during each day that the group recrossed its own path and averaging these over the five-day sample period. Ranks of both measures were correlated ($r_s = 0.57, p < 0.05$). As expected, the group recrossed its path more often in months when animals spent more time foraging on plant than on animal material ($r_s = 0.60, p < 0.05$). The correlation between number of path crossings and time feeding on fruit was also significant ($r_s = 0.70, p < 0.01$). Average turning angle, however, did not correlate with the importance of fruit in the daily diet ($r_s = 0.24, p > 0.05$), nor with the ratio of time feeding on plant versus animal material ($r_s = 0.10, p > 0.05$).

These results indicate that the movements of the capuchin group are not determined by simple rules conditional on the foraging experience or the allocation of foraging time of group members. There was no evidence of responses appropriate to area-restricted searches, though the tendency to backtrack varied appropriately with the resource being exploited. If the capuchin group was searching for resources, it was not showing the responses predicted by optimal

search models. It is also noteworthy that movements showed no overall directional asymmetry (Table 14), a characteristic that should increase searching efficiency (Cody, 1971; Pyke, 1978b; Krebs, 1979).

The final set of predictions (6a, 6b) derive from models that assume that animals know where resources are located. Some models postulate that a forager can evaluate the location and richness of various resource patches within its perceptual field (Pyke, 1978a; Waddington and Heinrich, 1979); others assume that animals rely on long-term memory of resource availability and distribution (Altmann and Altmann, 1970; S. Altmann, 1974; Kamil, 1978; Milton, 1980; Sigg and Stolba, 1981). Animals are "familiar with the major topography of their home range," and are able to "navigate within it on the basis of that familiarity" (Altmann and Altmann, 1970:198). Long-term spatial memory is certainly within the capacity of many invertebrates. Cognitive or mental maps were explored first in laboratory rodents in the 1940s by Tolman and his associates (reviewed in Tolman, 1948) and more recently by Olton (Olton and Samuelson, 1976; Olton, 1979). With these models, the animals' problem is not finding resources, nor maximizing encounter rate with prey or food patches, but rather moving so as to minimize travel time per unit of food intake. This involves the capacity to evaluate distances to resources, the spatial relationships among these resources, and the relative yield of each (Altmann's (1974) "n-step evaluator").

To evaluate the predictions, I needed to know the abundance and spatial distribution of the specific resources available each month. This posed two practical problems. First, in a complex environment and with an animal that has a catholic diet, I had to assume that a resource was available if some animal ate it. This would introduce a bias if items were not eaten that were available. In this low-diversity forest, however, few items that seemed to be appropriate monkey food were available at any time, and none of these were conspicuously ignored. Second, there are a number of food items used by animals in a

group in a given month. Which were the most important determinants of a group's movement? If more than one item is considered, how should they be weighted? I excluded all items of animal origin, for the distribution of these is relatively homogeneous and they probably have little effect on movements. To avoid the problem of weighting availabilities and preferences for different plant items, I also excluded all but the most commonly taken item. In most months, the single most commonly taken plant item, always the fruit of a tree species, constituted a large fraction of all items taken, both plant and animal (see Table 8). In two months, December 1977 and 1978, the most commonly taken item constituted less than 15% of all items, so these months were excluded from the analysis.

Prediction 6a: Daily path length should correlate positively with the patchiness of the single plant species most fully represented in the diet, for the reasons stated in prediction 4b. In addition, feeding on a highly patchy species should encourage heterogeneous movements, as the group moves quickly between patches, and remains for long periods within each patch.

Results were as expected. In months when the plant item most fully represented in the diet was patchy, daily path length was long ($r = 0.77$, $p < 0.01$). Variance in step lengths (H'_i) within each month correlates significantly across months with the Morisita's index of the most used species of fruiting tree ($r = 0.68$, $p < 0.05$).

Prediction 6b: In addition to species patchiness (= consistency, or degree to which trees are grouped in space), species clumping (the extent to which tree groups are clumped in space) might affect group movements. As interpatch distances increase, a group might respond in one of two ways. Either it should move the long distances between patches, or it could ignore distance patches choosing to remain in the vicinity of a single patch, to which it returns at regular intervals. In the first case, daily path length should increase, and average

turning angle and turning angle diversity should decrease with interpatch distance. In the second case, the reverse would be true. In accord with both cases, daily path length is negatively correlated with both average turning angle ($r = -0.66$, $p < 0.01$) and with turning angle diversity ($r = -0.52$, $p < 0.05$).

As an index of clumping, I used the previously calculated spread index. As Morisita's index and the spread index are independent of each other ($r = -0.002$, for the 14 tree species most commonly used by capuchins), the effects of each can be analyzed separately. Ranked spread index values of the most used fruit species in each month were negatively correlated with average daily path length ($r = -0.43$, $p < 0.05$), and positively with average turning angle ($r = 0.37$, $p > 0.05$) and turning angle diversity ($r = 0.53$, $p < 0.05$). As the spread of patches increases, groups tend not to move between patches but remain in the vicinity of a single patch.

In summary, these hypotheses of how groups move represent extremes on a continuum. It is unlikely that animals know nothing about the area in which they live beyond their immediate perceptions and sensations, especially if animals have stable ranges, well-travelled pathways, and habitual sleeping and drinking sites. On the other hand, animals certainly do not know everything about their range, for there is considerable variability in resource availability across days, months, and years. Yet, the strong relationship between the movements of the capuchin group and the distribution of the specific food used in each month indicates that animals have considerable knowledge of the location of their resources and can move accordingly.

USE OF SPACE

If there is a definable area over which the group ranges, then the number of new quadrats entered should decline with time, and eventually reach an asymptote. Figure 19 plots the cumulative increase in quadrat area over 14 monthly sample periods. After 72 complete days, the cu-

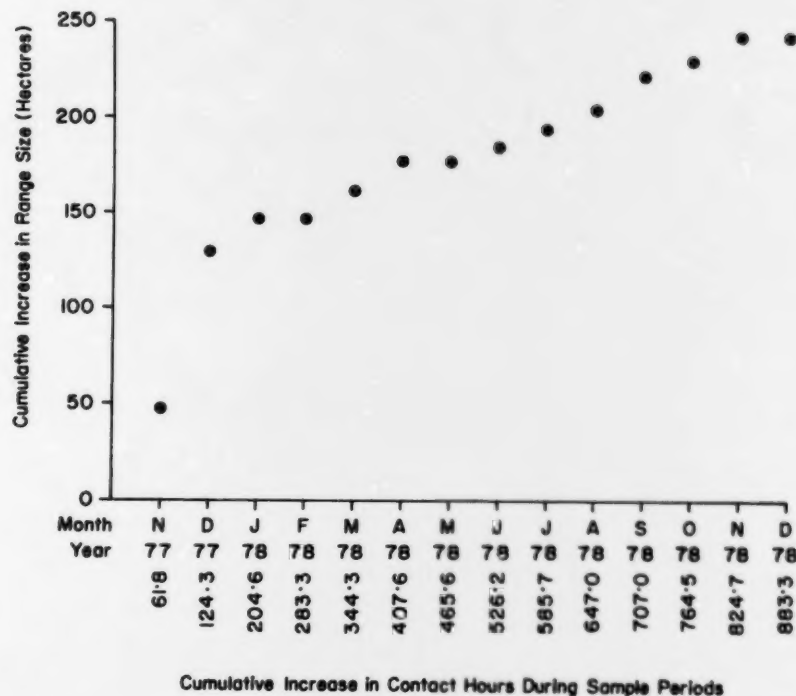


FIGURE 19.—Cumulative area occupied by the study group, restricted to areas entered during the five-day periods at the beginning of each month.

mulative area had reached 243 ha and showed little tendency to reach an asymptote. At the end of the study reported here (July 1979), including 27 partial days of mapped movement, the total home range area had reached 257 ha (1,374 contact hours). Since then no systematic location data have been collected, but as of June 1982, total area has increased to perhaps 275 ha (1,545 contact hours).

Use of space is related to group movements. The number of hectares occupied each month correlates positively with average daily path length ($r_s = 0.60$, $p < 0.05$), and negatively with average monthly turning angle ($r_s = -0.84$, $p < 0.01$). When the group is moving rapidly and not backtracking, it enters more areas.

As the group's movements are not random, neither is the use of space. Figure 20 plots the number of quadrats against their frequency of use. If quadrat use was random and independent

of other quadrats, then this frequency distribution should follow a zero-truncated Poisson distribution (see Cohen, 1971). The distribution is truncated at zero because, in theory, some quadrats remain undiscovered, though in this case the distribution predicts no missing quadrats. There is little relation between observed and expected. Some quadrats were used much more than predicted, others much less. This is also evident when examining quadrat use in the home range (Figure 21). Relatively few quadrats are used intensely, many are used infrequently. Quadrats of high use are clumped in two major centers and not distributed randomly across the range. Figure 22 shows the cumulative hours of occupancy plotted against a ranked ordering of quadrats. The extent to which this curve deviates from a straight line joining the first and last points indicates the degree of unevenness of range use. The group spent 50% of its time in only

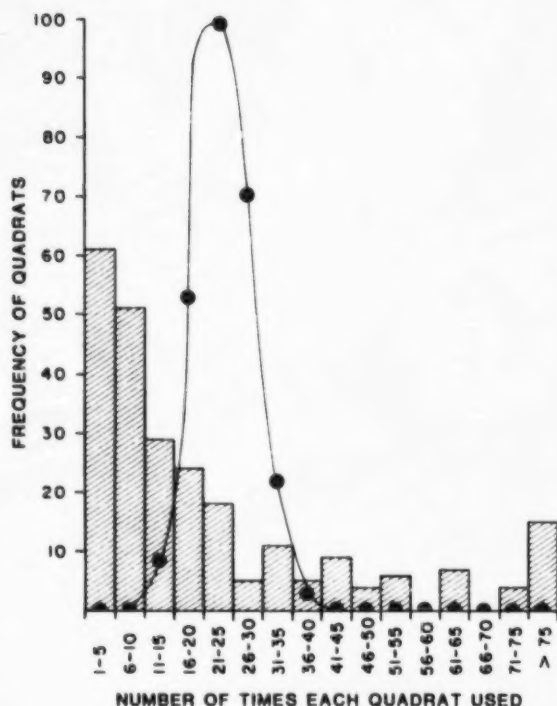


FIGURE 20.—Frequency distribution of quadrat intensity of use. Closed circles are the distribution expected if occupancy were random (following a Poisson distribution).

15% of the home range, and 75% of its time in 31% of the total area.

SEASONAL VARIATION.—Simple indices of variation, such as the Shannon-Wiener index of diversity H' (Struhsaker, 1974; Oates, 1977) or Rasmussen's index RU (Rasmussen, 1979, 1980) can also measure variation in range use. RU , in addition to measuring the consistency or patchiness of range use (how unevenly quadrats are used), includes the effect of clumping or grain (how quadrats of high use are aggregated), and is used here. Table 15 presents the area used and the RU index of range use for each of the 14 months of the study. Monthly variation in these measures is negatively correlated ($r_s = -0.66$, $p < 0.01$). This relationship accords with that found by Rasmussen (1979) for baboons. The RU index correlates positively with the average turning angle across months ($r_s = 0.86$, $p < 0.01$)

and negatively with path length ($r_s = -0.52$, $p < 0.05$), confirming that in months when the group moved long distances but did not backtrack, both the number of new areas entered and the evenness of quadrat use were high. Thus I expected resource availabilities to also determine use of space.

Prediction 7: Use of space should correlate with the spatial distribution of trees used in each month. In a given month, the group should spend more time in areas where tree density of those species in fruit is highest.

I restricted the analysis to tree species that each accounted for over 10% of the plant items taken in a given month. The frequencies that trees of these 11 species were found in the hectare quadrats were correlated with the time the group occupied quadrats in each month. Figure 10, for instance, plots the monthly correlation coefficients (r_{xy}) for *Guazuma tomentosa*. In the dry season months, January through March, when fruit was available, the group was likely to be found in high-density *Guazuma* areas. The correlation coefficients in this analysis were never high because during the five-day monthly samples the group only entered an average of 26% of the total range, but they were often statistically significant ($r = 0.16$ at the 5% confidence level and 0.21 at the 1% level). Figures 9–11 present coefficients for the other 10 species. Because of intercorrelations among spatial distributions of tree species, in some months the group used areas even though the local fruits were not available. For instance, *Vitex orinocensis*, *Annona jahnii*, and *Randia hebecarpa* all occur on *medano* sand ridges (Troth, 1979). The *Randia* distribution correlates with that of *Vitex* ($r = 0.47$, $p < 0.01$) and with *Annona* ($r = 0.17$, $p < 0.05$), and the distribution of *Vitex* closely matches that of *Annona* ($r = 0.39$, $p < 0.01$). Therefore range use correlates with the distribution of each of these species during months when any of the three were in fruit. In general however, in months when a tree species is in fruit, the group's use of space matches its spatial distribution.

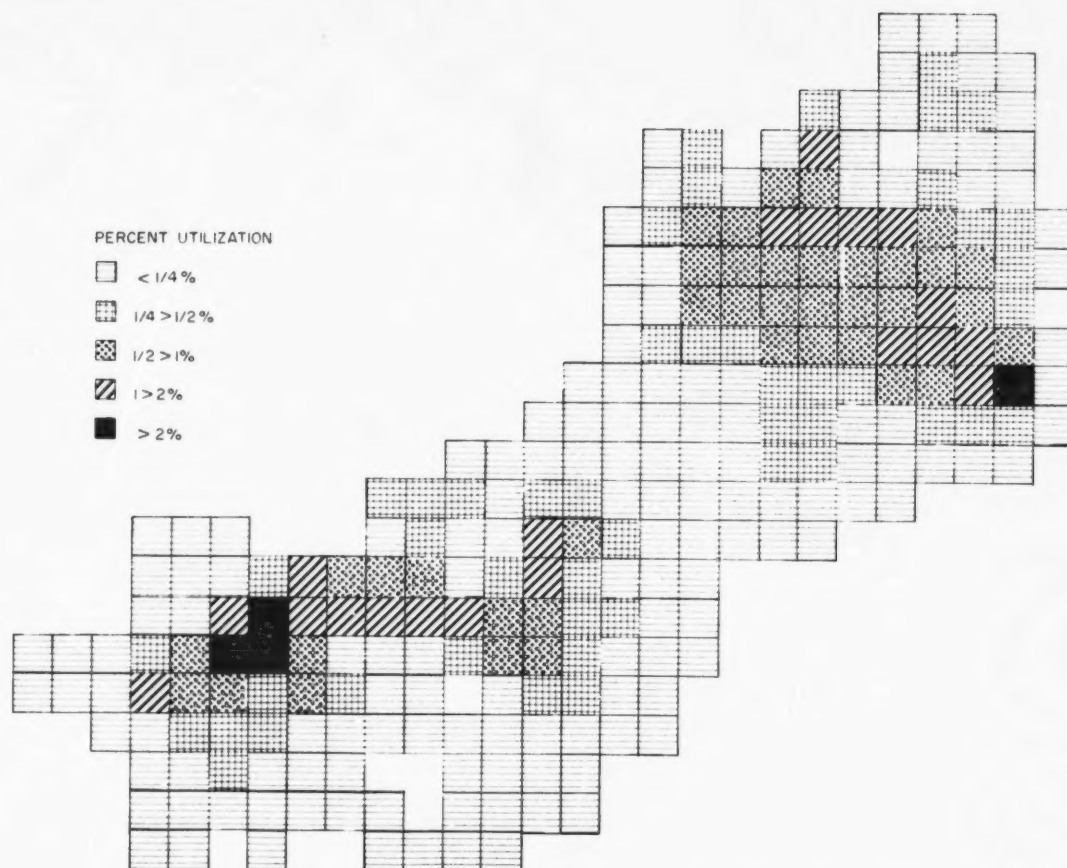


FIGURE 21. —Quadrat occupation, placing each quadrat in one of five intensities of use.

How resource availability affects use of space is less clear. If animals have information on resource abundance for the area or patch where they actually are, and the environment as a whole, then some time allocation models predict that animals should remain in that area until their foraging success falls to the marginal value equal to the average foraging success for the environment as a whole (Charnov, 1976; Pyke et al., 1977; Krebs, 1979). At that point they should leave the area and begin searching for a new one. Animals will spend more time in areas or patches rich in resources (Waser and Wiley, 1979; McNair, 1982) and less time in poor areas. This mechanism requires only that animals have the

capacity to evaluate resource abundance, presumably through variation in their foraging success, and integrate their foraging success over a period of time. It follows that:

Prediction 8a: An uneven spatial distribution of resources should result in an uneven use of space. The more patchy the resource distribution, the longer animals should remain in given patches before moving, and the more heterogeneous should be the use of space.

Fruits are patchily distributed in the forest, while invertebrates are scattered relatively homogeneously. Contrary to prediction, unevenness of range use, as measured by the *RU* index,

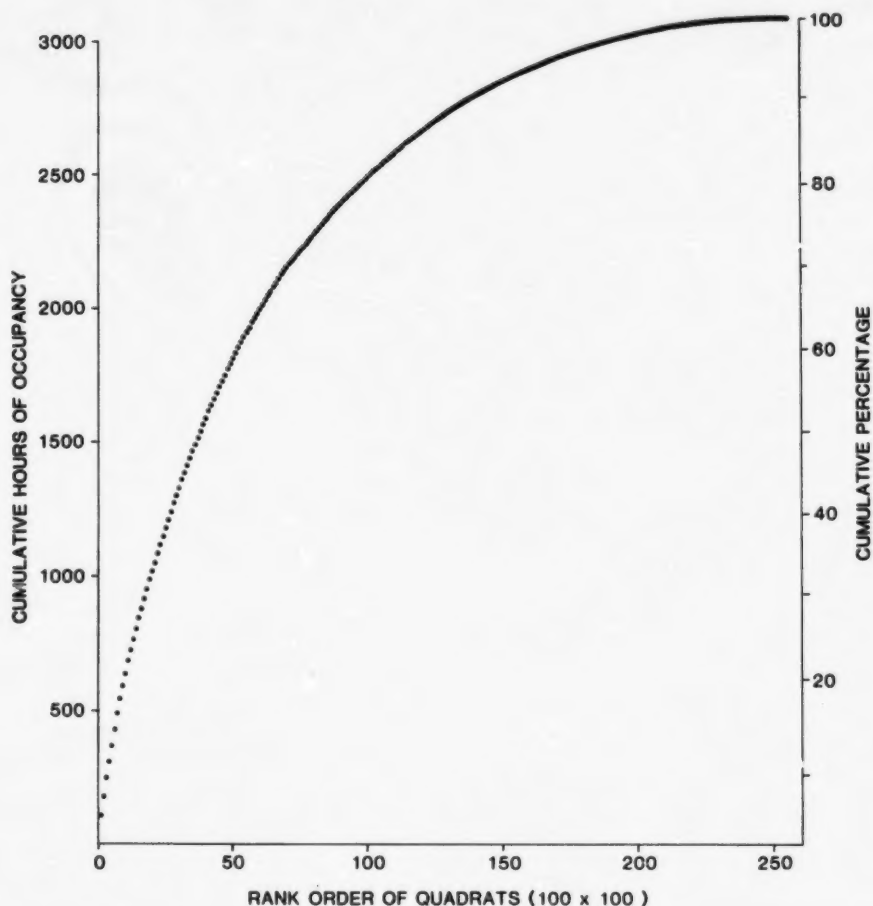


FIGURE 22.—Distribution of the duration of quadrat occupancy. Figure plots cumulative hours of occupancy against a ranked order of quadrats.

did not correlate with fruit foraging time ($r_s = 0.03$, $p > 0.05$), nor with foraging time taking invertebrates ($r_s = 0.02$, $p > 0.05$).

An alternative hypothesis is that animals have information of patch quality and location. Animals should leave a patch when their expected foraging success will be higher if they move to another patch of known quality and location (S. Altmann, 1974). If, before leaving a patch, animals only evaluate the location and quality of single patches, but do not take into account the spatial relationships of one patch to another (S. Altmann's "one-step evaluator"), then it follows

that:

Prediction 8b: An uneven spatial distribution of the specific resource most used at given time should result in an uneven use of space. If, as previously suggested, the capuchin group moves in response to the location and quality of resource patches, then animals might also have the capacity to allocate time to patches depending on location and quality of other nearby patches.

Contrary to expectation, unevenness of range use, as measured by the *RU* index, did not cor-

TABLE 15.—Use of space during 5-day systematic samples.

Mpnth	Area used (ha)	Rank	<i>RU</i> index of clumping	Rank
1977				
Nov	46	11	4.61	4
Dec	105	1	2.03	13
1978				
Jan	44	12	4.68	3
Feb	31	13	4.77	2
Mar	69	7	2.76	7
Apr	86	5	2.49	9
May	50	10	3.13	5
Jun	52	9	5.74	1
Jul	28	14	3.12	6
Aug	61	8	2.13	12
Sep	100	3	2.39	10
Oct	89	4	2.38	11
Nov	104	2	2.60	8
Dec	75	6	1.71	14

relate with the spatial unevenness (also measured by the *RU* index) of the single most commonly used plant item in each month ($r_s = -0.30$, $p > 0.05$). Any tendency is opposite to that predicted.

This result does not conclusively reject this hypothesis. If the decision to leave a patch takes into account the spatial relationship among patches (greater than one-step evaluation), then it might be more efficient to move to a nearby poor patch and ignore a distant rich one. In this case, a simple correlation between the unevenness of use of space and that of specific resources would not be expected.

Another hypothesis is that the frequency and location of intergroup encounters limit a group's use of space (Struhsaker, 1974). Home ranges of different groups overlap completely. All locations within the range of the study group were visited by at least one other group. Other groups did not avoid areas intensively used by the study group; rather, the probability of encountering another group in resource-rich areas was disproportionately high. While it is impossible to calculate the isolation field of the main group (Waser and Wiley, 1979) because the use of space by other groups is not known, it appears likely that there is no correlation between this group's

activity and isolation field. Figure 23 plots the location of my first contact for the nine other *Cebus* groups that overlapped the main group's range. At least three other groups were encountered, though more rarely, in this range. Despite this overlap and high concentration of groups, intergroup encounters were uncommon. During the 1,860 contact hours with all capuchin groups to date (June 1982), I have noted only 72 intergroup interactions. Outcomes of interactions were independent of their location, but did depend on the identities of groups. Table 16 shows a clear rank order in outcomes of interactions among nine groups that interacted with the Main group.

Prediction 9: Because the study group was high-ranking, its use of space should be little affected by the frequency of intergroup encounters.

There was no correlation between the frequency of intergroup interactions and either the total area used each month ($r_s = 0.14$, $p > 0.05$) or Rasmussen index of range clumping ($r_s = 0.02$, $p > 0.05$).

This is not to say that the use of space of high ranking groups is totally unaffected by inter-

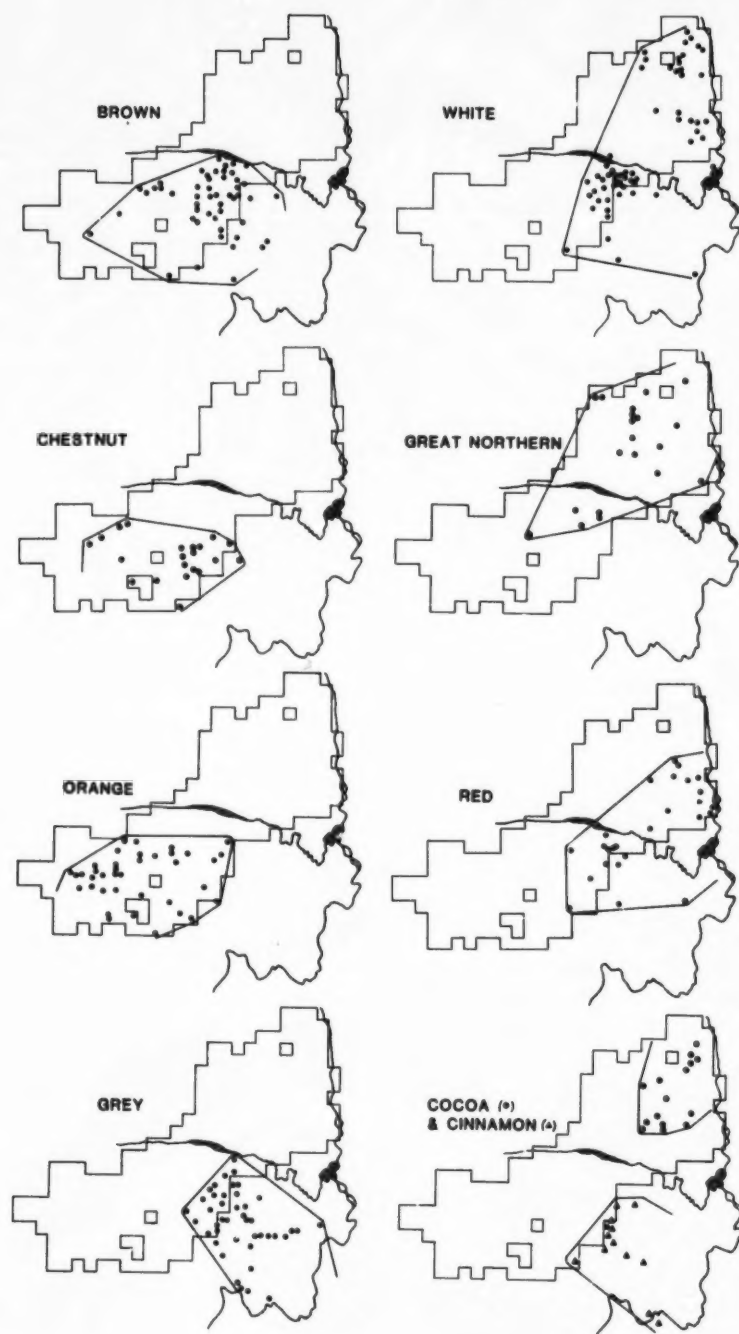


FIGURE 23.—Overlap of the main study group's range with those of nine other groups. Main group's range defined by quadrats used on all eight maps of the study area. Ranges of other groups are defined by closed circles marking the location of the first encounter with each group and a "taut-string" line enclosing these locations.

TABLE 16.—Outcome of intergroup encounters (June 1977–June 1982).

Winner	Loser										
	Cinnamon	Northern	Main	Chestnut	Grey	Orange	Cocoa	Red	White	Brown	Unknown
Cinnamon			1		1				1		
Northern			4					1			
Main				2	3	7	2	5	7	2	21
Chestnut			1								
Grey						1			1	1	1
Orange			3							1	
Cocoa								1			
Red									2		
White										1	
Brown											
Unknown			2								
Group size at last census	>40	>40	28	15	19	22	16	28	10	10	

group interactions: There was possibly a tendency for the winning group not to move into the area previously occupied by the other, and the long-term consequence of interactions is mutual avoidance. In addition, the low rate of intergroup interactions suggest that low ranking, usually small groups, successfully avoid encounters in most cases.

In summary, use of space is not correlated with the frequency of intergroup interactions, at least for the high ranking study group, but is correlated with the distribution of the resources available in each month. The behavioral mechanism responsible for this correlation remains unclear.

Discussion

Social organization and diet are related in primates presumably because the diet of a species determines how animals forage, and how animals forage limits the possible social alternatives (but see Freeland, 1976; Rasmussen, 1979; van Schaik, 1983). One general assumption is that the potential diet of a species (what animals can eat) in a specific habitat determines both the abundance of available resources, and the patchiness and grain of the resource distribution. Resources are more abundant and less patchy for a

generalist than a specialist. There is less agreement on how these resource availabilities determine foraging behavior.

Some foraging models have focussed on resource abundance. Overall resource abundance determines the time allocated to foraging, and the abundance of specific resources determines the allocation of foraging time to each (Pyke et al., 1977; Krebs, 1979). Animals forage on items and in areas that give them the greatest immediate energetic return. Partitioning of available time into moving and feeding, in turn, determines group movements and use of space (Cody, 1971; Pyke et al. 1977). These models generally share the assumption that animals have information on the abundances of specific resources in the environment, but do not know where resources are located. Studies of the economy of time in primates include those of Hladik (1977), Coelho et al. (1976), Milton (1980), and Gaulin and Gaulin (1982). This approach has generated models of group size (e.g., Caraco, 1979a, 1979b; Barnard, 1980; Bertram, 1980; Brown, 1982) that consider group size as constrained by the partitioning of available time among different activities.

Other models have focussed on resource distribution. Movements and use of space are not

consequences of how time is allocated to take advantage of variation in resource abundance, but are responses to resource distributions (Altmann and Altmann, 1970; Harding, 1973; Clutton-Brock, 1975b; Sigg and Stolba, 1981). Some of these models assume that animals have considerable knowledge of the location of resources in their environment. This additional information might allow foraging animals to defer immediate gain if it is to their long-term advantage. This approach has generated models of social groups (e.g., S. Altmann, 1974; Bradbury and Vehrencamp, 1976; Waser and Wiley, 1979; Leighton and Leighton, 1982) that consider group size as a response to the spatial distribution of resources.

This study of the wedge-capped capuchin monkey *Cebus olivaceus* examined predictions derived from these foraging models. Overall resource abundance was a poor predictor of time allocated to foraging, especially during the wet season when there was no scarcity of food. Time allocated to foraging, both in general and on specific food items, was a poor predictor of group movements and use of space. Instead, animals responded spatially to the specific spatial distributions of specific resources. What characteristics of the animal and the environment encourage these behavioral responses?

DIET.—*Cebus olivaceus* is a ripe-fruit specialist. Ripe fruits make up the plant diet even in the dry season when fruit availability is low. Its two congeners, *C. albifrons* (Defler, 1979a; Terborgh, 1983) and *C. capucinus* (Oppenheimer, 1968) show similar dietary preferences. In contrast, *C. apella* shifts from ripe fruit to palm nuts and plant pith in period of low availability (Terborgh, 1983).

Reliance on ripe fruit has a number of consequences. Fruits occur only in fruiting trees, and most species are patchily distributed in space. At any given time, fruits occur in only a few distinct localities. Animals must therefore cross areas poor in resources in moving between rich food patches. In most, if not all areas, fruits are also seasonally abundant (Foster, 1973; Foster, 1977; Struhsaker, 1978; Leigh et al., 1983; this study).

Fruit specialists must therefore survive an annual fruit bottleneck. With the exception of asynchronously fruiting trees such as figs, most species fruit at regular intervals. Therefore, at a given time, the locations of fruiting trees are predictable.

Invertebrates are also a significant part of the diet, especially in months when fruit is not available. Capuchins forage for invertebrates as they move between fruit trees. Fruits and invertebrates, however, are not interchangeable food items. The time devoted to invertebrate foraging rarely falls below 20% of the monthly time budget. Ripe fruits are generally low in protein (Foster, 1977; Milton, 1981; Vellayan, 1981), a deficiency that can be remedied by taking invertebrates. Even when a fruit tree is not exhausted, the capuchin group will through the day, repeatedly leave the tree to forage for invertebrates.

One major consequence of insectivory is that it increases the time that must be allocated for foraging. Foraging for invertebrates is time consuming, and this imposes constraints on the amount of time available for other activities. On an annual basis, for instance, 33% of the items taken were invertebrates, but capuchins spent 55% of their time foraging for these items.

USE OF TIME.—It is therefore not surprising that only during the dry season, when invertebrate foraging is most important, does foraging time reflect resource abundance. During the wet season, in contrast, both invertebrate and fruit resources are abundant. Foraging time reflects the digestive capacities of the monkeys: capuchins stock up for the next period of food scarcity.

GROUP MOVEMENTS AND USE OF SPACE.—Foraging for invertebrates is not an important determinant of use of space because invertebrates are distributed relatively homogeneously in space. Fruits, in contrast, are scattered through the environment. To efficiently exploit such resources, capuchins must have an effective searching mechanism or they must know the location of resources. The best searching formation is a long rank of individuals spread out perpendicu-

lar to the line of group movement (S. Altmann, 1974). Group spread in *C. olivaceus* is considerable, often extending over 150 m, but animals tend not to move in a rank (Robinson, 1981). Another way to search is to rely on the noise of other successful foraging species. Capuchin groups might be attracted to certain trees by noisy birds such as Chachalacas *Ortalis ruficauda*, Parakeets *Aratinga pertinax* and *Brotogeris jugularis*, and Caciques *Cacicus cela*. Many species of trees used by monkeys, however, do not attract birds. When, in addition, the fruiting species is uncommon and/or patchily distributed, non-directed searching would be unsuccessful. Indeed, the analysis of *Cebus* group movements indicates that animals are familiar with the location of resources. Familiarity with a certain area and the location of resources in that area has been posited as one of the major selective advantages of maintaining a range over time and avoiding new areas (Zach and Falls, 1976a, 1976b, 1976c; Waser and Wiley, 1979).

There are two spatial responses, not necessarily mutually exclusive, that animals can take to fruit bottlenecks. (1) They can become less discriminating as to what food they will accept (MacArthur and Pianka, 1966; Charnov, 1976). This is the response taken by *C. apella* (Terborgh, 1983). (2) They can relocate to areas with resources, in which case the home range must be large enough to encompass the edaphic conditions and vegetation characteristics necessary to ensure that at least one species is in fruit at all times. These movements can be considerable, as in the long-distance migrations of some animals (Bergerud, 1974; Gaines and McClenaghan, 1980; Fretwell, 1980). A number of primate species, including *C. olivaceus*, that rely on ripe fruit respond in this manner, e.g., mangabeys (*Cercocebus albigena*; Waser, 1977); woolly monkeys (*Lagothrix*; Durham, 1972); spider monkeys (*Ateles*; Klein and Klein, 1977); and pig-tailed macaques (*Macaca nemestrina*; Caldecott, 1981). All have large home ranges.

GROUP SIZE.—Foraging characteristics potentially affect the social characteristics of a species.

Ripe fruit occurs in discrete patches. Patch size might limit group size (Kummer, 1968; S. Altmann, 1974; Jarman, 1974; Bradbury and Vehrencamp, 1976; Waser, 1977; Leighton and Leighton, 1982; Terborgh, 1983). Spatially restricted resources might allow dominant animals to monopolize the resource (e.g., Willis, 1967; Robinson, 1981). Variance in feeding success within the group should then increase with group size, and decrease with patch size. Group size should be limited because subordinates will be encouraged to leave the group as their foraging success diminishes (Vehrencamp, 1979). Interpatch distance might also limit group size (Rodman, 1980). If individuals form subgroups when all group members cannot simultaneously use a patch, then as the spread of patches increases, so does the cost of forming subgroups. This should encourage permanent splitting of large groups. Neither of these arguments, however, accounts for the variation in group size in the genus *Cebus*. Group size in *C. apella* is much smaller (Külhorn, 1939; Thorington, 1967; Klein and Klein, 1975; Izawa, 1980; Terborgh, 1983) than in the non-tufted capuchins (Oppenheimer, 1968; Defler, 1979b; this study). It is the non-tufted capuchins that are the ripe fruit specialists, and thus should experience greater interpatch distances. Neither is patch size a determinant: *C. apella* differs, not by relying on smaller fruit trees, but by being less selective during the fruit bottleneck (Terborgh, 1983).

What is it about a ripe fruit specialist of this body size that encourages a large group relative to congeners? Large groups might have a search advantage (Eisenberg et al., 1972; Izawa, 1979). *C. olivaceus* groups are frequently familiar with the location of resources, however, so this is probably a minor consideration. A related idea is that there are more individuals familiar with resource locations in large groups. The complete tolerance of old, non-reproductive individuals, both male and female, in *C. olivaceus* groups might support this. Such animals were recorded in most study groups. Non-reproductive females have also been recorded in the mangabey, an-

other ripe fruit specialist with large groups and large ranges. Perhaps most important, however, is that in species with large ranges, which rely on resources that are spatially aggregated, widely distributed, and frequently uncommon, group ranges tend to overlap considerably. The potential for intergroup competition at fruit trees is high (Wrangham, 1980). Many intergroup encounters occur in the vicinity of fruit trees, and vocal playback experiments (Robinson, 1985b) indicate that groups respond to mimicked neighbors more aggressively, and move away less readily, while feeding in fruit trees than when foraging for invertebrates. Dominant groups were

large and subordinate groups small. Therefore a major selective advantage to living in a large group is the ability to displace smaller groups at fruit trees, which presumably compensates for the increased within-group competition at food resources.

Group size, then, is both directly and indirectly affected by the spatial distribution of resources. The size and distribution of resource patches influence the ability of groups to monopolize these resources, and group movements and use of space, which also depend on the spatial distribution of food, influence the probability of encountering other groups.

Appendix I

Glossary of *Cebus olivaceus* Foraging Actions

Bang: using hands; holds object and repeatedly brings it down on a substrate; commonly with snails, certain fruits.

Bang and bite: combination action.

Break: using hands; holds object in both hands and exerts a lateral shear force; commonly with twigs, small branches.

Bite: using teeth; either places object directly into mouth or bites into substrate to split open (e.g., to reach grubs inside branches) or to shatter (e.g., to reach grubs inside old palm fruits); commonly with cryptic invertebrates.

Bite and break: combination action.

Carry: usually with a hand but sometimes in the mouth; obvious.

Chew: using mouth; obvious.

Dig: using hands and often teeth; objects commonly embedded in the ground (*Cochlospermum* seedlings, *Pomacea* snails), under debris in tree cavities or palm crowns.

Examine: visual; inspects potential foraging substrate or food item.

Feel: using hands and relying on touch; inspects potential foraging substrate or food item.

Grab: using hands; rapid (as opposed to the slower *take*) hand movement to grasp usually non-cryptic, motile invertebrate prey; commonly grasshoppers, cockroaches, etc.

Lick: using tongue; commonly water from streams, off leaves, etc., but also small items such as scale insects, egg cases, etc.

Masticate: using teeth; chews but does not ingest food item, which is expelled finally; commonly the pith of palm fronds, orchid leaves, probably primarily for water content.

Mouth: using lips and tongue; takes object into mouth without use of hands; commonly certain species of fruits (e.g., *Zanthoxylum*) and non-motile, cryptic invertebrate prey.

Open: using hands, pulls apart object, often delicately; commonly fruits (e.g., *Capparis*, *Sterculia*).

Pick: using hands; plucks item and ingests; exclusively fruits.

Pursue: obvious.

Rip: using hands; tear apart substrate to expose prey objects; commonly to reach grubs, etc., in rotting wood.

Rip and bite: combination action.

Roll: using hands; object is moved backward and forward along a substrate; commonly to remove noxious hairs, etc., from food item.

Scan: visual; look over foraging substrate, though not as intently as *examine*; turning head from side to side.

Sift: using hands with close visual attention; methodically examine a substrate, passing objects through hands; commonly in leaf litter on the ground or in the crown of palm trees.

Sniff: olfactory; obvious.

Tap: using knuckles or fingernails; rap on substrate to locate food items; commonly grub or ant cavities inside twigs or branches, and inside old palm fruits.

Tap and bite: combination action.

Take: using hands; slow hand movement to grasp usually cryptic, non-motile prey; commonly caterpillars, beetles, etc.

Turn over: using hands; objects are turned over to reveal hidden side; commonly palm fronds to expose invertebrate prey.

Appendix II

Microhabitats

Use of different microhabitats when foraging for animals. For each habitat the method of capture is specified.

Microhabitat	Foraging movement	Animal identified	Animal not identified	Unknown	Total
Palm frond	Slow: mouthing, taking, sifting from surface	11	50	10	82
Palm top	Rapid: grabbing from surface	4	7		
	Slow: digging, sifting into crown, taking items	2	119	10	147
Palm boot	Rapid: grabbing from surface	11	5		
	Breaking open hollow boot by ripping, biting, and banging	36	32		79
	Slow: mouthing, taking from surface	6	1		
	Rapid: grabbing from surface	4			
Between palm boots	Digging between boots, ripping out boots	3	93		119
	Slow: taking of items from exposed surface	3	1	5	
	Rapid: grabbing from exposed surface	14			
Dead, dried palm fronds	Biting and breaking the dry rachis	20	15		170
	Slow: sifting through fronds, taking items, mouthing	11	81	4	
	Rapid: grabbing	3	13		
	Turning over to expose underside		23		
Tree trunks (>15 mm diameter)	Slow: examining and taking		10	1	14
	Rapid: grabbing	3			
Tree branches (5-15 mm in diameter)	Tapping, then ripping and biting to expose inside	14	17	1	173
	Slow: mouthing or taking off exposed surface	105	5	3	
	Rapid: grabbing	12	16		
Tree twigs (<5 mm diameter)	Tapping, then ripping, biting, and breaking to expose inside	70	153	1	244
	Slow: mouthing or taking off exposed surface	11	2	7	
Underside of trunk or branch	Slow: feeding, mouthing, taking	6	3	3	26
	Rapid: grabbing		12	2	
Leaves	Slow: sifting, mouthing, taking, licking items from surface	229	23	156	490

Appendix II.—Continued.

Microhabitat	Foraging movement	Animal identified	Animal not identified	Unknown	Total
Bromeliad	Rapid: grabbing	5	76	1	6
	Slow: sifting		2		
Dead trunk	Rapid: grabbing	4			20
	Digging into and ripping apart rotting material	8	7		
Dead branch	Slow: taking		1		54
	Rapid: grabbing	1	1		
	Turning over to get at underside		2		
	Digging into, biting and ripping apart rotting material	9	18		
	Slow: mouthing and taking	25			
Dead twig	Rapid: grabbing	1			41
	Turning over		1		
	Biting and digging into	2	9		
Dead leaves still in tree	Slow: taking	30			62
	Slow: sifting, taking, and mouthing	17	19	13	
Dead leaves on ground	Rapid: grabbing	1	12		587
	Slow: sifting and taking	430	45	1	
	Rapid: grabbing	110		1	
Under bark	Ripping off bark (especially of <i>P. tortum</i>)	3	25		35
	Taking items from in bark	5	2		
Under bark of dead trunks or branches	Biting, digging and ripping off bark	3	8		11
Old fruit (<i>Ficus trigonata</i> and <i>Cordia collococca</i>)	Biting into old fruit to expose invertebrates		9		9
Old fruit (<i>Copernicia tectorum</i>)	Cracking open nut, removing grub with mouth or fingernail		115		115
Seed pod	Splitting pod and mouthing items		7		7
Tree bole	Digging into	1	7		9
	Grabbing rapidly into	1			
Flowers	Sifting through and taking items	2	1		3
Crevasse in trunk	Digging into		5		
	Rapid: grabbing	2			7
Termite nest	Ripping apart		2		6
	Slow: mouthing and taking	3		1	
Bird's nest	Taking eggs, nestlings	22			23
	Sifting through nest materials		1		
Earth	Sifting through and taking items	1	1		2
Standing ground water	Slow: taking	32	3		37
	Rapid: grabbing		1	1	
Wasp's nest, under branches, twigs, leaves, palm fronds		92			92
Unknown		34	54	275	363
Totals		1422	1115	496	3033

Appendix III

Plant Species Used by Capuchins

AMARYLLIDACEAE

Hymenocallis venezuelensis Traub

ANACARDIACEAE

Spondias mombin L.

ANNONACEAE

Annona jahnii Safford

ARECACEAE

Copernicia tectorum (H.B.K.) Martius

ASCLEPIADACEAE

Marsdenia undulata (Jacquin) Dugand

BIGNONIACEAE

Macfadyena uncata (Andrews) Sprague & Sandwith

BORAGINACEAE

Cordia collococca L.

Cordia polycephala (Lamarck) Johnston

BROMELIACEAE

Bromelia chrysantha Jacquin

Bromelia plumieri (E. Morris) L.B. Smith

CACTACEAE

Hylocereus polyrhizus Britton and Rose

CAPPARACEAE

Capparis corcolobifolia Martius

Capparis odoratissima Jacquin

COCHLOSPERMACEAE

Cochlospermum vitifolium (Willdenow) Sprengel

COMBRETACEAE

Combretum fruticosum (Loefling) Stuntz

CONNARACEAE

Connarus venezuelanus Baillon

CUCURBITACEAE

Luffa operculata (L.) Cogniaux

Melothria trilobata Cogniaux

CYPERACEAE

Scleria setuloso-ciliata Boeckeler

DILLENIACEAE

Tetracera volubilis L.

EBENACEAE

Diospyros ierensis Britton

EUPHORBIACEAE

Dalechampia scandens L.

Margaritaria nobilis L.f.

FABACEAE (CAESALPINOIDEAE)

Copaifera officinalis H.B.K.

Hymenaea courbaril L.

FABACEAE (MIMOSOIDEAE)

Albizia guachapele (H.B.K.) Dugand

Entada polystachya DC.

Pithecellobium daulense Spruce ex Benth

Pithecellobium guaricense Pittier

Pithecellobium saman (Jacquin) Benth

FABACEAE (FABOIDEAE)

Centrosema pubescens Benth

Machaerium moritzianum Benth

FLACOURTIACEAE

Hecastostemon completus (Jacquin) Sleumer

GRAMINAE

Lacisias anomala Hitchcock

LORANTHACEAE

Phoradendron sp.

MALPIGHIACEAE

Malpighia emarginata DC.

MALVACEAE

Wissadula periplocifolia (L.) Presl

MARANTACEAE

Thalia geniculata L.

MELIACEAE

Trichilia trifolia L. subspecies *trifolia*

MORACEAE

Cecropia sp.

Chlorophora tinctoria (L.) Gaudichaud

Ficus pertusa L.f.

Ficus trigonata L.

Ficus sp.

OCHNACEAE

Ouratea guildingii (Planchon) Urban

ORCHIDACEAE

Oncidium cebolleta (Jacquin) Benth

Oncidium carthaginense (Jacquin) Swartz

PASSIFLORACEAE

Passiflora serrulata Jacquin

POLYGONACEAE

Coccoloba caracasana Meisner

ROSACEAE

Licania apetala (E. Meyer) Fritsch.

RUBIACEAE

- Chomelia spinosa* Jacquin
Genipa americana L. var. *caruto* (H.B.K.) K. Schumann
Guettarda divaricata (Humboldt and Bonpland ex Roemer
and Schultes) Standley
Psychotria anceps H.B.K.
Randia hebecarpa Benth
Randia venezuelensis Steyermark

RUTACEAE

- Zanthoxylum culantrillo* H.B.K.

SAPINDACEAE

- Allophylus cobbe* Leenhouts

- Paullinia cururu* L.

STERCULIACEAE

- Guazuma tomentosa* H.B.K.
Sterculia apetala (Jacquin) Karsten

VERBENACEAE

- Vitex capitata* Vahl
Vitex compressa Turczaninow
Vitex orinocensis var. *multiflora* (Miquel) Huber, vel. sp. aff.

VITACEAE

- Cissus alata* Jacquin
Cissus sicyoides L.

Literature Cited

- Altmann, J.
1974. Observational Study of Behaviour: Sampling Methods. *Behaviour*, 49:227-267.
- Altmann, S.A.
1974. Baboon, Space, Time, and Energy. *American Zoologist*, 14:221-248.
- Altmann, S.A., and J. Altmann
1970. *Baboon Ecology: African Field Research*. 220 pages, Chicago: University of Chicago Press.
- Archibald, E.E.A.
1949. The Specific Character of Plant Communities, II: A Quantitative Approach. *Journal of Ecology*, 37:274-288.
- Aristeguieta, L.
1966. Florula de la Estación Biológica de Los Llanos. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, 26:228-307.
- August, P.
1981. Fig Fruit Consumption and Seed Dispersal by *Artibeus jamaicensis* in the Llanos of Venezuela. *Reproductive Botany, Biotropica*, 13(Suppl.):70-76.
- Barnard, C.J.
1980. Equilibrium Flock Size and Factors Affecting Arrival and Departure in Feeding House Sparrows. *Animal Behaviour*, 28:503-511.
- Batschelet, E.
1965. Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms. *American Institute of Biological Sciences Monograph*. 57 pages, Washington, D.C.
1972. Recent Statistical Methods for Orientation Data. In S.G. Galler, K. Schmidt-Koenig, J.G. Jacobs, and R.E. Belleville, editors, *Animal Orientation and Navigation*, pages 61-91. Washington, D.C.: NASA.
- Bergerud, A.T.
1974. The Role of the Environment in the Aggregation, Movement and Disturbance Behaviour of Caribou. In B. Geist and F. Walther, editors, *The Behavior of Ungulates and Its Relation to Management*, pages 552-584. Morges: IUCN Publications.
- Bertram, B.C.
1980. Vigilance and Group Size in Ostriches. *Animal Behaviour*, 28:278-286.
- Bradbury, J., and S. Vehrencamp
1976. Social Organization and Foraging in Emballonurid Bats, II: A Model for the Determination of Group Size. *Behavioral Ecology and Sociobiology*, 1:383-404.
- Brinker, R.C.
1969. *Elementary Surveying*. Scranton: International Textbook Company.
- Brown, J.L.
1982. Optimal Group Size in Territorial Animals. *Journal of Theoretical Biology*, 95:793-810.
- Buskirk, R.E., and W.H. Buskirk
1976. Changes in Arthropod Abundance in a Highland Costa Rican Forest. *American Midland Naturalist*, 95:288-298.
- Caldecott, J.O.
1981. Findings on the Behavioural Ecology of the Pig-tailed Macaque. *Malaysian Applied Biology*, 10:213-220.
- Caraco, T.
1979a. Time Budgeting and Group Size: A Theory. *Ecology*, 60:611-617.
1979b. Time Budgeting and Group Size: A Test of Theory. *Ecology*, 60:618-627.
- Castillo, S.
1977. Estudio de una sección del bosque de galería del Río Orituco al sur de los llanos de Calabozo. Unpublished Licenciado thesis, Universidad Central de Venezuela, Caracas, Venezuela.
- Charnov, E.L.
1976. Optimal Foraging: The Marginal Value Theorem. *Theoretical Population Biology*, 9:129-136.
- Charnov, E.L., G.H. Orians, and K. Hyatt
1976. The Ecological Implications of Resource Depression. *American Naturalist*, 110:141-151.
- Chivers, D.J.
1974. The Siamang in Malaya: A Field Study of a Primate in Tropical Rain Forest. *Contributions to Primatology*, 4:1-335.
- Clutton-Brock, T.H.
1974. Primate Social Organization and Ecology. *Nature*, 250:539-542.
1975a. Feeding Behavior of Red Colobus and Black and White Colobus in East Africa. *Folia Primatologica*, 23:165-207.
1975b. Ranging Behaviour of Red Colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Animal Behaviour*, 23:706-722.
1977. Some Aspects of Intraspecific Variation in Feeding and Ranging Behaviour in Primates. In T.H. Clutton-Brock, editor, *Primate Ecology*, pages 539-

556. New York: Academic Press.
- Clutton-Brock, T.H., and P.H. Harvey
1983. The Functional Significance of Variation in Body Size Among Mammals. In J.F. Eisenberg and D. Kleiman, editors, *Advances in the Study of Mammalian Behavior*, *American Society of Mammalogists Special Publication*, 7:632-659. Shippensburg.
- Cody, M.L.
1971. Finch Flocks in the Mohave Desert. *Theoretical Population Biology*, 2:142-158.
- Coelho, A.M., Jr., C.A. Bramblett, L.B. Quick, and S.S. Bramblett
1976. Resource Availability and Population Density in Primates: A Socio-bioenergetic Analysis of the Energy Budgets of Guatemalan Howler and Spider Monkeys. *Primates*, 17:63-80.
- Cohen, J.E.
1971. *Casual Groups of Monkeys and Men*. 171 pages, Cambridge, Massachusetts: Harvard University Press.
- Crook, J.H., and J.S. Gartlan
1966. Evolution of Primate Societies. *Nature*, 210:1200-1203.
- Curtis, J.T., and R.P. McIntosh
1951. An Upland Forest Continuum in the Prairie-forest Border Region of Wisconsin. *Ecology*, 32:476-496.
- Defler, T.R.
1979a. On the Ecology and Behavior of *Cebus albifrons* in Eastern Colombia, I: Ecology. *Primates*, 20:475-490.
1979b. On the Ecology and Behavior of *Cebus albifrons* in Eastern Colombia, II: Behavior. *Primates*, 20:491-502.
- De Vita, J., D. Kelly, and S. Payne
1982. Arthropod Encounter Rate: A Null Model Based on Random Motion. *American Naturalist*, 119:499-510.
- Durham, N.M.
1972. Grouping Behavior in Wild Woolly Monkeys, *Lagothrix lagotricha*, of Southern Peru [abstract]. *American Journal of Physical Anthropology*, 37:435.
- Eisenberg, J.F., N.A. Muckenhirn, and R. Rudran
1972. The Relation between Ecology and Social Structure in Primates. *Science*, 176:863-874.
- Emlen, J.M.
1966. The Role Of Time and Energy in Food Preference. *American Naturalist*, 100:611-617.
- Ewel, J.J., A. Madriz, and J.A. Tosi
1976. *Zonas de vida de Venezuela*. 270 pages, Caracas: Editorial Sucre.
- Foster, M.S.
1977. Ecological and Nutritional Effects of Food Scarcity on a Tropical Frugivorous Bird and Its Food Source. *Ecology*, 58:73-85.
- Foster, R.B.
1973. Seasonality of Fruit Production and Seedfall in a Lowland Forest Ecosystem in Panama. Doctoral dissertation, Duke University.
1980. Heterogeneity and Disturbance in Tropical Vegetation. In M.E. Soulé and D.A. Wilcox, editors, *Conservation Biology, An Evolutionary-Ecological Perspective*, pages 75-92. Sunderland: Sinauer.
- Fragaszy, D.
In press. Time Budgets and Foraging Behavior in Wedge-capped Capuchins (*Cebus nigrivittatus*): Age and Sex Differences. In *Proceedings of the Ninth International Congress of Primatology, 1982, Volume 1: Current Perspectives in Primate Social Dynamics*. New York: Van Nostrand.
- Freeland, W.J.
1976. Pathogens and the Evolution of Primate Sociality. *Biotropica*, 8:12-24.
- Fretwell, S.
1980. Evolution of Migration in Relation to Factors Regulating Bird Numbers. In A. Keast and G. Morton, editors, *Migrant Birds in the Neotropics; Ecology, Behavior, Distribution, and Conservation*, pages 517-528. Washington, D.C.: Smithsonian Institution Press.
- Gaines, M.S., and L.R. McClenaghan
1980. Dispersal in Small Mammals. *Annual Review of Ecology and Systematics*, 11:163-196.
- Gaulin, S.J.C., and C.K. Gaulin
1982. Behavioral Ecology of *Alouatta seniculus* in Andean Cloud Forest. *International Journal of Primatology*, 3:1-52.
- Harding, R.S.
1973. Range Utilization by a Troop of Olive Baboons (*Papio anubis*). Doctoral dissertation, University of California, Berkeley.
- Hassell, M.P.
1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton: Princeton University Press.
- Hladik, A., and C.M. Hladik
1969. Rapports trophiques entre végétation et primates dans la forêt de Barro-Colorado (Panama). *La Terre et la Vie*, 25:25-117.
- Hladik, C.M.
1977. A Comparative Study of the Feeding Strategies of Two Sympatric Species of Leaf Monkeys: *Presbytis senex* and *Presbytis entellus*. In T.H. Clutton-Brock, editor, *Primate Ecology*, pages 324-354. New York: Academic Press.
- Honacki, J.H., K.E. Kinman, and J.W. Koeppel
1982. *Mammal Species of the World: A Taxonomic and Geographic Reference*. Lawrence: Allen Press and the Association of Systematic Collections.
- Hubbell, S.P.
1979. Tree Dispersion, Abundance and Diversity in a

- Tropical Dry Forest. *Science*, 203:1299-1309.
- Izawa, K.
 1979. Foods and Feeding Behavior of Wild Black-capped Capuchin (*Cebus apella*). *Primates*, 20:57-76.
 1980. Social Behavior of the Wild Black-capped Capuchin (*Cebus apella*). *Primates*, 21:443-467.
- Izawa, K., and A. Mizuno
 1977. Palm-fruit Cracking Behavior of Wild Black-capped Capuchin (*Cebus apella*). *Primates*, 18:773-792.
- Jacobs, J.
 1974. Quantitative Measurement of Food Selection: A Modification of the Forage Ratio and Ivlev's Electivity Index. *Oecologia*, 14:413-417.
- Janis, C.
 1976. The Evolutionary Strategy of the Equidae and the Origins of Rumen and Cecal Digestion. *Evolution*, 30:457-476.
- Janzen, D.H.
 1973. Sweep Samples of Tropical Foliage Insects: Effects of Seasons, Vegetation Types, Elevation, Time of Day, and Insularity. *Ecology*, 54:687-708.
- Jarman, P.S.
 1974. The Social Organization of Antelope in Relation to Their Ecology. *Behaviour*, 48:215-267.
- Kamil, A.C.
 1978. Systematic Foraging by a Nectar Feeding Bird, the Amakihi (*Loxops virens*). *Journal of Comparative and Physiological Psychology*, 92:388-396.
- Klein, L.L., and D.B. Klein
 1975. Social and Ecological Contrast Between Four Taxa of Neotropical Primates. In R.H. Tuttle, editor, *Socioecology and Psychology of Primates*, pages 59-85. Chicago: Aldine.
 1977. Feeding Behaviour of the Colombian Spider Monkey. In T.H. Clutton-Brock, editor, *Primate Ecology*, pages 153-182. New York: Academic Press.
- Krebs, J.R.
 1979. Foraging Strategies and Their Social Significance. In P. Marler and J.G. Vandenbergh, editors, *Handbook of Neurobiology*, 3 (Social Behavior and Communication):225-270. New York: Plenum Press.
- Kühlhorn, F.
 1939. Beobachtungen über das Verhalten von Kapuzineraffen in Freier Wildbahn. *Zeitschrift für Tierpsychologie*, 3:147-151.
- Kummer, H.
 1968. *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press.
- Leigh, E.G., Jr., A.S. Rand, and D.M. Windsor, editors
 1983. *Ecology of a Neotropical Forest: Seasonal Rhythms and Long-term Changes*. Washington, D.C.: Smithsonian Institution Press.
- Leighton, M., and D.R. Leighton
 1982. The Relationship of Size of Feeding Aggregate to Size of Food Patch: Howler Monkeys (*Alouatta palliata*) Feeding in *Trichilia cipo* Fruit Trees on Barro Colorado Island. *Biotropica*, 14:81-90.
- MacArthur, R.H., and E.R. Pianka
 1966. On Optimal Use of Patchy Environment. *American Naturalist*, 100:603-609.
- Mader, W.J.
 1979. First Nest Description for the Genus *Micrastur* (Forest Falcons). *Condor*, 81:320.
- McNab, B.K.
 1983. Ecological and Behavioral Consequences of Adaptation to Various Food Resources. In J.F. Eisenberg and D. Kleiman, editors, *Advances in the Study of Mammalian Behavior, American Society of Mammalogists Special Publication*, 7:664-697. Shippensburg.
- McNair, J.N.
 1982. Optimal Giving-Up Times and the Marginal Value Theorem. *American Naturalist*, 119:511-529.
- Miguela, P.
 1969. Bioenergetics of Pregnancy and Lactation in the European Common Vole. *Acta Theriologica*, 14:167-179.
- Milton, K.
 1980. *The Foraging Strategy of Howler Monkeys*. New York: Columbia.
 1981. Food Choice and Digestive Strategies of Two Sympatric Primate Species. *American Naturalist*, 117:496-505.
- Monasterio, M., and G. Sarmiento
 1976. Phenological Strategies of Plant Species in the Tropical Savanna and the Semi-deciduous Forest of the Venezuelan Llanos. *Journal of Biogeography*, 3:325-356.
- Montgomery, G.G., and Y.L. Lubin
 1977. Prey Influences on Movements of Neotropical Anteaters. In R.L. Phillips and C. Jonkel, editors, *Proceedings of the 1975 Predator Symposium*, pages 103-131. Missoula: University of Montana Press.
- Muller-Schwarze, D., B. Staggs, and C. Muller-Schwarze
 1982. Play Behavior: Persistence, Decrease, and Energetic Compensation During Food Shortage in Deer Fawns. *Science*, 215:85-87.
- Oates, J.F.
 1977. The Guereza and Its Food. In T.H. Clutton-Brock, editor, *Primate Ecology*, pages 276-321. New York: Academic Press.
- Olton, D.S.
 1979. Mazes, Maps, and Memory. *American Psychologist*, 34:583-596.
- Olton, D.S., and R.J. Samuelson
 1976. Remembrance of Places Passed: Spatial Memory

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- in Rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 2:97-116.
- Oppenheimer, J.R.
1968. Behavior and Ecology of the White-Faced Monkey, *Cebus capucinus*, on Barro Colorado Island, C.Z. Doctoral dissertation, University of Illinois.
- Orlosky, F.J.
1981. Dental Evolutionary Trends of Relevance to the Origin and Dispersion of the Platyrrhine Monkeys. In R.L. Ciochon and A.B. Chiarelli, editors, *Evolutionary Biology of the New World Monkeys and Continental Drift*, pages 189-200. New York: Plenum.
- Poole, R.W.
1974. *An Introduction to Quantitative Ecology*. New York: McGraw-Hill.
- Post, D.G.
1981. Activity Patterns of Yellow Baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Animal Behaviour*, 29:357-374.
- Pyke, G.H.
1978a. Optimal foraging: Movement Patterns of Bumblebees Between Inflorescences. *Theoretical Population Biology*, 13:72-98.
1978b. Are Animals Efficient Harvesters? *Animal Behaviour*, 26:241-250.
1981. Optimal Foraging in Hummingbirds: Rules of Movement Between Inflorescences. *Animal Behaviour*, 29:889-896.
- Pyke, G.H., R. Pulliam, and E.L. Charnov
1977. Optimal Foraging: A Selective Review of Theory and Tests. *Quarterly Review of Biology*, 52:137-154.
- Raemaekers, J.
1980. Causes of Variation Between Months in the Distance Traveled Daily by Gibbons. *Folia Primatologica*, 34:46-60.
- Ramia, M.
1974. *Plantas de las sabanas llaneras*. 289 pages, Caracas: Monte Avila Editores.
- Rasmussen, D.R.
1979. Correlates of Patterns of Range Use of a Troop of Yellow Baboons (*Papio cynocephalus*), I: Sleeping Sites, Impregnable Females, Births, and Male Emigrations and Immigrations. *Animal Behaviour*, 27:1098-1112.
1980. Clumping and Consistency in Primates' Patterns of Range Use: Definitions, Sampling, Assessment, and Applications. *Folia Primatologica*, 34:111-139.
- Robinson, J.G.
1979. Correlates of Urine Washing in the Wedge-capped Capuchin *Cebus nigrivittatus*. In J.F. Eisenberg, editor, *Vertebrate Ecology in the Northern Neotropics*, pages 137-143. Washington, D.C.: Smithsonian Institution Press.
1981. Spatial Structure in Foraging Groups of Wedge-capped Capuchin Monkeys, *Cebus nigrivittatus*. *Animal Behaviour*, 29:1036-1056.
- 1985a. Diurnal Variation in Foraging and Diet in the Wedge-capped Capuchin *Cebus olivaceus*. *Folia Primatologica*, 43:216-228.
1985b. Expected Benefits Determine Area Defense: Experiments with Capuchin Monkeys. *National Geographic Research Report*, 21:421-424.
- Rodman, P.S.
1980. Group Size of Forest Primates in Relation to Food Dispersion [abstract]. *American Journal of Physical Anthropology*, 53:271.
- Rudran, R.
1978. Socioecology of the Blue Monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology*, 249: 88 pages, 34 figures.
- Schaik, C.P. van
1983. Why Are Diurnal Primates Living in Groups? *Behaviour*, 87:120-144.
- Schoener, T.W.
1971. The Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*, 2:369-404.
- Sigg, H., and A. Stolba
1981. Home Range and Daily March in a Hamadryas Baboon Troop. *Folia Primatologica*, 36:40-75.
- Smith, J.N.M.
1974a. The Food Searching Behavior of Two European Thrushes, I: Description and Analysis of Search Paths. *Behaviour*, 48:276-302.
1974b. The Food Searching Behavior of Two European Thrushes, II: The Adaptiveness of Search Patterns. *Behaviour*, 49:1-61.
- Snow, D.W., and B.K. Snow
1964. Breeding Seasons and Annual Cycles of Trinidad Land-birds. *Zoologica*, 49:1-35.
- Sokal, R.R., and F.J. Rohlf
1969. *Biometry*. San Francisco: Freeman.
- Struhsaker, T.T.
1974. Correlates of Ranging Behavior in a Group of Red Colobus Monkey (*Colobus badius tephrosceles*). *American Zoologist*, 14:177-184.
1975. *The Red Colobus Monkey*. Chicago: University of Chicago Press.
1978. Food Habits of Five Monkey Species in the Kibale Forest, Uganda. In D.J. Chivers and J. Herbert, editors, *Recent Advances in Primatology*, 1(Behavior):225-228. New York: Academic Press.
- Struhsaker, T.T., and L. Leland
1977. Palm-nut Smashing by *Cebus a. apella* in Columbia. *Biotropica*, 9:124-126.
1979. Socioecology of Five Sympatric Species in the Kibale Forest, Uganda. *Advances in the Study of*

- Behavior*, 9:159-228.
- Studier, E.H., V.L. Lysengen, and M.J. O'Farrell
1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae), II: Bioenergetics of Pregnancy and Lactation. *Comparative Biochemistry and Physiology*, 44A:467-471.
- Taylor, T.W.
1978. Forest-soil Relationships of the Western Llanos of Venezuela. Doctoral dissertation, Texas A & M University.
- Terborgh, J.W.
1983. *Five New World Primates*. Princeton: Princeton University Press.
- Thomas, G.
1974. The Influence of Encountering a Food Object on Subsequent Searching Behavior in *Gasterosteus aculeatus* (L.). *Animal Behaviour*, 22:941-952.
- Thorington, R.W., Jr.
1967. Feeding and Activity of *Cebus* and *Saimiri* in a Colombian Forest. In D. Stark, R. Schneider, and H.J. Kuhn, editors, *Progress in Primatology*, pages 180-184. Stuttgart: Fischer.
- Tolman, E.C.
1948. Cognitive Maps in Rats and Men. *Psychological Review*, 55:189-208.
- Troth Ovrebo, R.G.
1979. Vegetational Types on a Ranch in the Central Llanos of Venezuela. In J.F. Eisenberg, editor, *Vertebrate Ecology in the Northern Neotropics*, pages 17-30. Washington, D.C.: Smithsonian Institution Press.
- van Schaik, C.P. See Schaik, C.P. van.
- Vehrencamp, S.L.
1979. The Roles of Individual, Kin, and Group Selection in the Evolution of Sociality. In P. Marler and J.G. Vandenberg, editors, *Handbook of Behavioral Neurobiology*, 3(Social Behavior and Communication):351-394. New York: Plenum.
- Vellayan, S.
1981. The Nutritive Value of *Ficus* in the Diet of Lar Gibbon (*Hylobates lar*). *Malaysian Applied Biology*, 10:177-182.
- Waddington, K.D., and B. Heinrich
1979. The Foraging Movements of Bumblebees on Vertical "Inflorescences": An Experimental Analysis. *Journal of Comparative Physiology*, 134:113-117.
- Walter, H.
1971. *Ecology of Tropical and Subtropical Vegetation*. Edinburgh: Oliver and Boyd.
- Waser, P.M.
1976. *Cercopithecus albigena*: Site Attachment, Avoidance, and Intergroup Spacing. *American Naturalist*, 110:911-935.
1977. Feeding, Ranging, and Group Size in the Mangabey *Cercopithecus albigena*. In T.H. Clutton-Brock, editor, *Primate Ecology*, pages 183-222. New York: Academic Press.
1978. Postreproductive Survival and Behavior in a Free-ranging Female Mangabey. *Folia Primatologica*, 29:142-160.
1981. Sociality or Territorial Defense? The Influence of Resource Renewal. *Behavioral Ecology and Sociobiology*, 8:231-237.
1982. Primate Polyspecific Associations: Do They Occur by Chance? *Animal Behaviour*, 30:1-8.
- Waser, P.M., and O. Floody
1974. Ranging Patterns of the Mangabey, *Cercopithecus albigena* in the Kibale Forest, Uganda. *Zeitschrift für Tierpsychologie*, 35:85-101.
- Waser, P.M., and R.H. Wiley
1979. Mechanisms and Evolution of Spacing in Animals. In P. Marler and J.G. Vandenberg, editors, *Handbook of Behavioral Neurobiology*, 3 (Social Behavior and Communication):159-223. New York: Plenum Press.
- Whitten, A.J.
1982. Home Range Use by Kloss Gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Animal Behaviour*, 30:182-198.
- Wiley, R.H., and M.S. Wiley
1980. Spacing and Timing in the Nesting Ecology of a Tropical Blackbird: Comparison of Populations in Different Environments. *Ecological Monographs*, 50:153-178.
- Willis, E.O.
1967. The Behavior of Bicolored Antbirds. *University of California Publications in Zoology*, 27:1-132.
- Wolda, H.
1978. Seasonal Fluctuations in Rainfall, Food, and Abundance of Tropical Insects. *Journal of Animal Ecology*, 47:369-381.
1979. Abundance and Diversity of Homoptera in the Canopy of a Tropical Forest. *Ecological Entomology*, 4:181-190.
- Wrangham, R.
1980. An Ecological Model of Female-bonded Primate Groups. *Behaviour*, 75:262-300.
- Zach, R., and J.B. Falls
1976a. Foraging Behavior, Learning, and Exploration by Captive Ovenbirds (Aves: Parulidae). *Canadian Journal of Zoology*, 54:1880-1893.
1976b. Ovenbird (Aves: Parulidae) Hunting Behavior in a Patchy Environment: An Experimental Study. *Canadian Journal of Zoology*, 54:1863-1879.
1976c. Do Ovenbirds (Aves: Parulidae) Hunt by Expectation? *Canadian Journal of Zoology*, 54:1894-1903.
1977. Influence of Capturing a Prey on Subsequent Search in the Ovenbird (Aves: Parulidae). *Canadian Journal of Zoology*, 55:1958-1969.

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